EFFECTS OF DISTURBANCE BY CLIPPING ON TWO DISTINCT FORMS OF *ZOSTERA MARINA* L.

A

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By

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EFFECTS OF DISTURBANCE BY CLIPPING ON TWO DISTINCT FORMS OF *ZOSTER MARINA* L.

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ABSTRACT

Biweekly clipping of leaves was used as a type of disturbance to compare the responses of eelgrass (*Zostera marina*) in shallow and deep water to those predicted from a terrestrial ecosystem succession model. All clipped plants had lower leaf growth rates than controls. Clipped plants decreased root-rhizome biomass in shallow water, but not in deep-water stands during 1981. During 1982 (better weather), shallow-water plants increased leaf carbon concentrations; deep-water plants decreased root-rhizome biomass. Root-rhizome to leaf ratios (high in shallow water and low in deep water) and weather conditions appeared important in determining the response to clipping. All plants had similar nitrogen content. These responses were typical of those reported for the tropical turtle grass, but were contrary to differences in plant growth strategies and nutrient use predicted from some terrestrial ecosystem studies of other higher vascular plants.

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF TABLES

LIST OF TABLES (continued)

LIST OF TABLES (continued)

LIST OF APPENDICES

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INTRODUCTION

The processes of ecosystem succession commonly act upon a variety of plant and animal populations in a given habitat. Theoretically, the composition of dominant groups changes from colonizing to climax species in a fairly predictable fashion (Odum 1969). In rocky intertidal marine communities, succession is species replacement; patterns are determined and maintained by competition, predation, and disturbance (Connell and Slatyer 1977, Paine 1984, and Sousa 1984a). The rocky intertidal community is an open system to which nutrients are supplied and lost through the water column. In most terrestrial systems, however, changes in soil composition and nutrient retention, accompany the evolution of a climax community. Accumulation of biomass and nutrients in the canopy and forest floor results in a complex, ecologically stable system in which resources are conserved (Bormann and Likens 1979, Gorham et al. 1979).

McRoy and Lloyd (1981) suggest that seagrass ecosystem development possesses those traits commonly ascribed to terrestrial rather than marine succession. They cite several examples of the importance of sediment development in the establishment of mature seagrass stands, particularly, the wasting disease of the 1930's, which eliminated many Atlantic eelgrass (*Zostera marina*)

beds. The disease produced changes in shoreline ecology that lingered for 20 to 30 years before eelgrass stands fully recovered (Rasmussen 1977).

In tropical and subtropical environments, seagrass succession proceeds through several different species assemblages, as do terrestrial or intertidal communities (Williams and McRoy 1982, Kirkman 1985), but, in temperate and higher latitudes, *Zostera marina* often is both the colonizing and the climax species (den Hartog 1977). Morphological variation in *Zostera marina* from different habitats is great, but a typical pattern of increasing leaf length and width with increasing sediment organic content and/or water depth has been widely reported (Keller and Harris 1966, Harrison and Mann 1975, Jacobs 1979, Dennison and Alberte 1982, Short 1983b). A relationship between plant morphology and sediment development suggests a within-species succession.

Succession is often interupted by disturbance (Sprugel and Bormann 1981, Sousa 1984b, Likens 1985), therefore, experimental disturbance can be used to examine certain successional processes. For example, disturbance of a community characterized by colonizing species might produce little change in species composition, whereas, disturbance of a late-successional community might favor

invasion of earlier-successional species and community structure might change considerably. The degree of change observed after disturbance, and the speed with which the community returns to its original species composition, can indicate the nature of community stability and resilience (Holling 1973). A stable community or ecosystem is one which can absorb stress without changing community structure. A resilient system is one which returns quickly to pre-disturbance composition after the community structure has been altered. Many late-successional or climax communities are highly stable, but poorly resilient. Colonizing species are often quite resilient, but relatively unstable (Holling 1973).

In order to examine succession in the *Z. marina* ecosystem, two vegetated sites were selected in an Alaskan lagoon. These stands had been studied previously (Fig. 1) and their basic structure was known (Dennison 1979, Iizumi et al. 1980, Short 1983b). *Z. marina* plants in shallow water are short, biomass is low, density is high, and root-rhizome to leaf ratios are high. Short (1983a, 1983b) suggested that plant growth in this area is limited by nutrient availability. Both nutrient-limited growth and high root-rhizome to leaf ratios are characteristic of early- or mid-successional state in terrestrial ecosystems

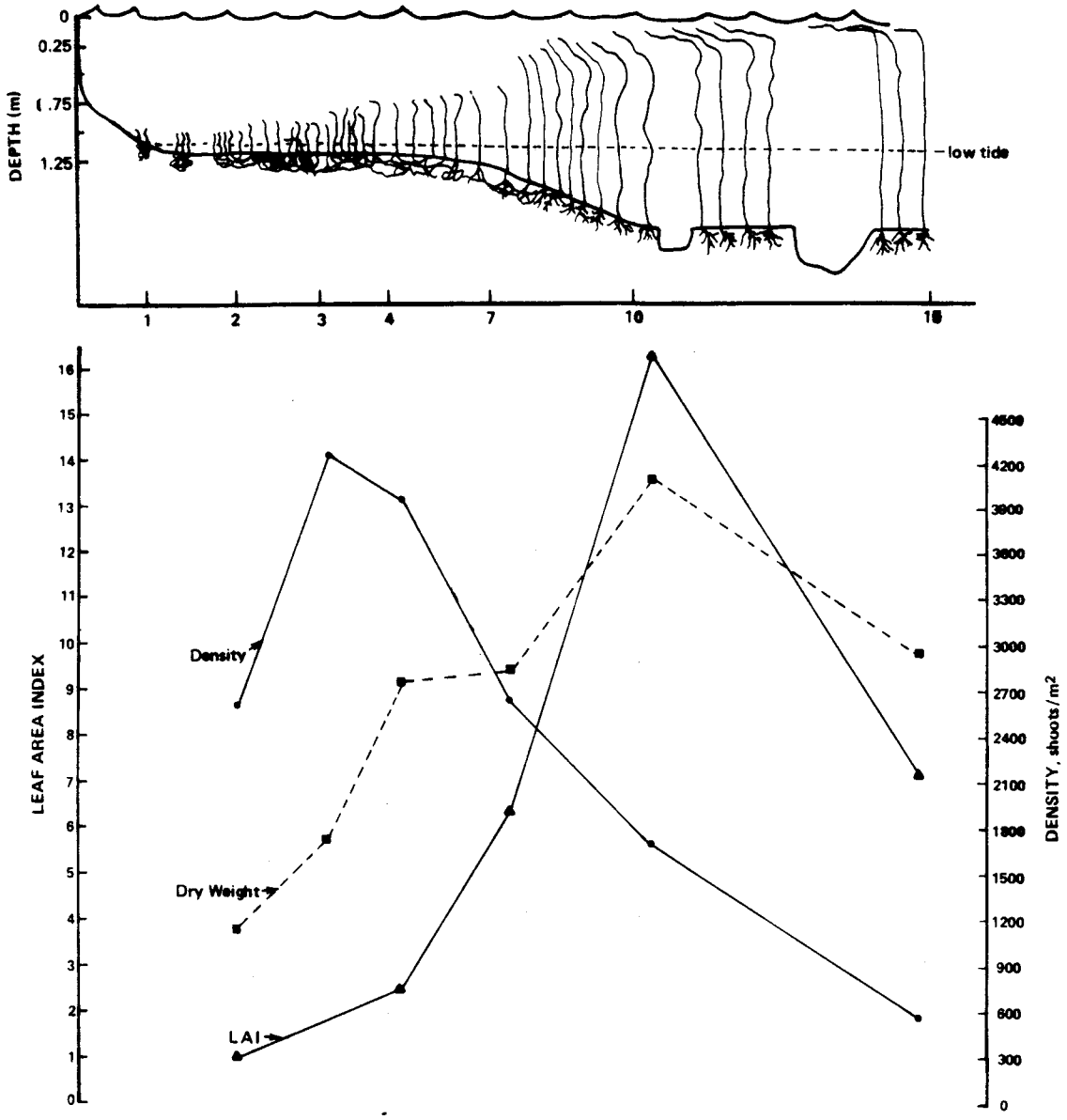

Fig. 1. Leaf area index, shoot density, and total dry weight of *Zostera marina* along the study transect in Izembek Lagoon, Alaska, July 1977, from Iizumi et al. (1984). Dry weights range from 350 to 1400 $g \cdot m^{-2}$.

(Mooney 1972, Grime 1979). In contrast, plants in deeper water are tall with higher total biomass, low density, low root-rhizome to leaf ratio, and light-limited growth (Dennison 1979). Light-limited growth is thought to be indicative of late-successional development in both seagrass (McRoy and McMillan 1977) and terrestrial ecosystems (Mooney 1972, Grime 1979). The responses of plants in these two areas to imposed disturbance were expected to differ if plant stands truely represented different successional states.

Clipping was chosen as the mode of disturbance because information on the tropical seagrass, *Thalassia testudinum*, indicated that grazing by turtles (*Chelonia mydas*) affected growth rates and carbohydrate reserves in rhizomes without killing plants (Greenway 1974, Zieman et al. 1984). Basic plant community parameters (e.g., biomass and density) within each *Z. marina* bed were evaluated before, during, and after clipping as indicators of the successional state of plants within the study plots. Leaf growth rates, carbon and nitrogen concentrations, and nitrogen uptake by roots were assessed to reveal processes of acclimation to clipping (i.e., did plant growth become either carbon or nitrogen limited after clipping?).

To test the theory that differences observed in *Z. marina* stands actually represent different systems of different successional state, the study examined two specific hypotheses:

1). *Zostera marina* stands in deep water in Izembek Lagoon (high biomass, low root-rhizome to leaf ratio, low density) are more stable than plants in shallow water (lower biomass, higher root-rhizome to leaf ratio, higher density).

2). Shallow-water plants are more resilient than deep-water plants.

Both hypotheses were tested by examining the cumulative effects of clipping through the summers of 1981, 1982, and November 1982 and April 1983.

METHODS

Site Description

Izembek Lagoon is situated near the tip of the Alaska Peninsula (55° 15'N, 163° 05'W). The lagoon covers approximately 218 km^2 and is densely populated by the seagrass *Zostera marina*. Two sites for experimental plots were selected from previously established stations near

Grant Point (Dennison 1979; Iizumi et al. 1980; Fig. 2). The original stations formed a transect describing plant morphological types commonly found in the lagoon. Plants closer to shore (Station 2) are typically short, approximately 30-35 cm; they occur in dense stands in low organic (approximately 3 % of dry wt [Short 1981]), muddy sediments. Plants farther offshore (Station 8) are long-leaved (85-90 cm) and are found growing more sparsely in high organic (approximately 6 % of dry wt [Short 1981]), muddy sediments.

The inshore area is within a perched depression in an otherwise gradually sloping terrace. As a result, plants at Station 2 remain submerged at all times. In 1981, depths measured at Station 2 during high (1.5 m above MLLW) and low (0.1 m above MLLW) tides were 81 and 19 cm, respectively. Because Station 8 is at a lower elevation, depths during the same tides were 120 and <5 cm, respectively. Tides changed more rapidly at Station 8 than at Station 2, and, as a result, plants at Station 8 were in deeper water than plants at Station 2 during 75 % of the tidal cycle.

The area around Station 8 was apparently elevated during the winter of 1981-1982. Qualitative observations revealed large changes in the duration of low tide between

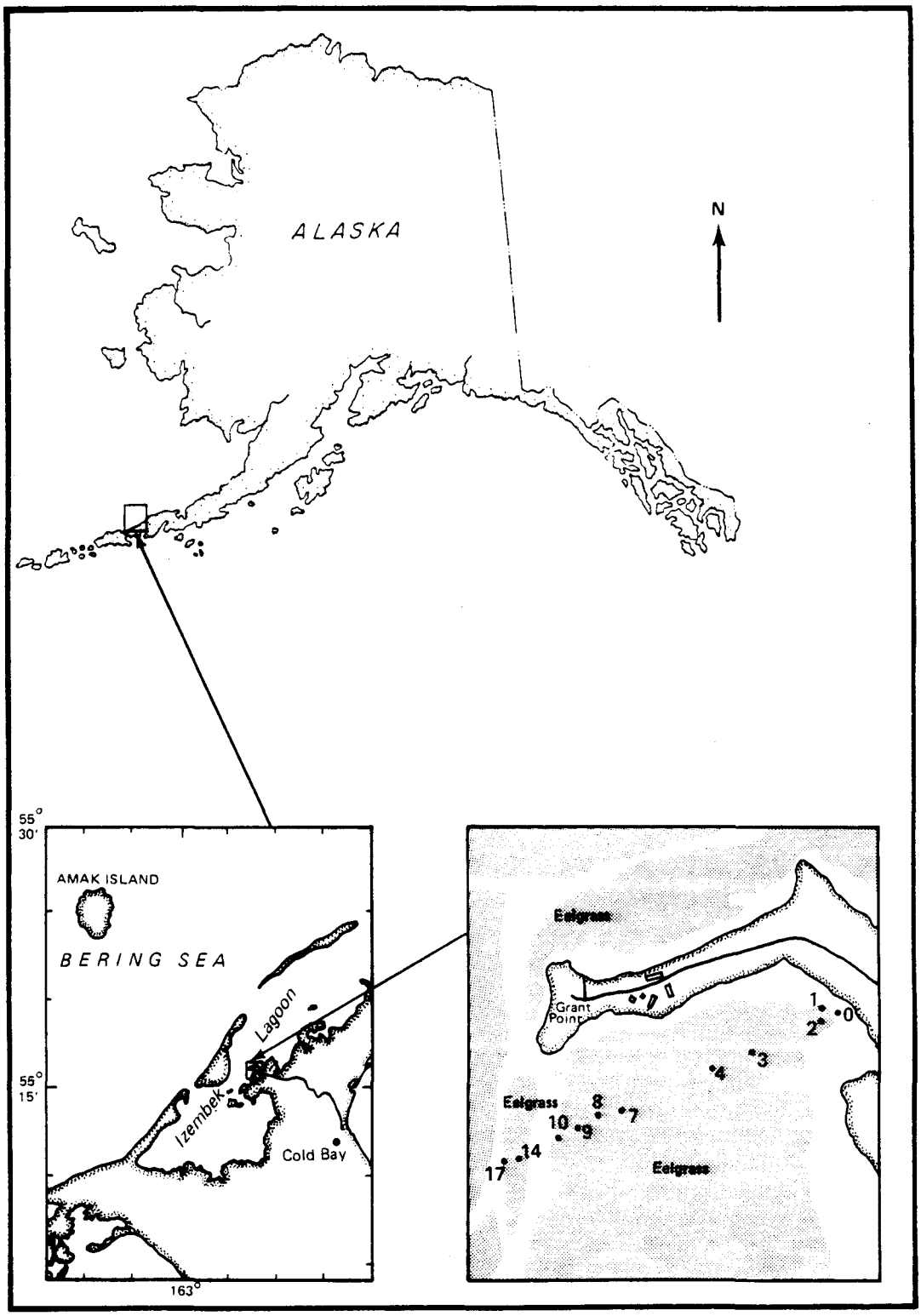

Fig. 2. Locations of Izembek Lagoon and the study transect at Grant Point.

1981 and 1982 at Station 8, but no differences at Station 2. Station 8 drained completely during most low tides in 1982 and remained exposed for approximately two hours during each lower low tide. In contrast, during 1981 this station was under shallow water (<15 cm) only briefly (<1 hr) during an average lower low tide. Longer exposure at low tide could have caused increased susceptibility to damage from ice. Ice scouring during the winter of 1981-1982 produced troughs of several meters in length and 10-20 cm in depth parallel to the transect in and around Station 8.

Clipping Experiments

At each station, a 100-m^2 plot was clipped approximately every ten days from June through August during 1981 and 1982. Plants were not clipped to an exact length, but were clipped to a height of 5-10 cm above the leaf sheath. Since plants at Station 8 were generally larger than those at Station 2, plant heights after clipping were approximately 15 cm at Station 2 and 20 cm at Station 8. Clipping was intended to stress the plants, not to damage them beyond the point of recovery. At the beginning of each season and prior to each successive clip, plant stands were sampled for biomass, density, and

chemical analysis using a 16 cm i.d. plexiglass corer. Plant stands were also sampled, but were not clipped, in November 1982 and April 1983.

Five replicate cores were taken in both clipped areas and surrounding control beds. Leaves were snipped at the sediment surface and placed in plastic bags with seawater. In the lab, leaf samples were separated into groups of reproductive and vegetative shoots, counted for density determination and dried at 60°C for 48 to 72 hr depending upon sample size. The root and rhizome component (which shall be referred to in this study as "roots-rhizomes" as distinguished from "roots" alone) was briefly washed of sediments using a screened box and placed in plastic bags with seawater. Roots-rhizomes were washed in tap water to remove sediments, and dried at 60°C for 48 to 72 hr. Mean seasonal ratios of below- to above-ground biomass were calculated from biomass data from this and previous studies in Izembek Lagoon (McRoy 1966, McRoy *unpublished*, Dennison 1979).

In 1982 and 1983, an additional core was taken at each site for carbon and nitrogen analyses of leaves and roots. Shoots were separated in the lab into groups of old and new leaves. A new leaf was defined as that most recently emerged from the leaf sheath. If this leaf was

less than 30 mm above the leaf sheath, the next oldest leaf was also considered new. All other green leaves were defined as old. Brown leaves were not analyzed. Leaves were rinsed in deionized water and cleaned of epiphytes; epiphytic diatoms were abundant in November 1982 and April 1983, but not during either summer. Root-rhizome samples for carbon and nitrogen analyses were cleaned of sediment as were biomass samples. All plant material for carbon and nitrogen analyses was freeze-dried and shipped to Fairbanks. Immediately prior to analysis all samples were freeze-dried again to remove any accumulated moisture. Independent subsamples were taken from each original sample, ground with a mortar and pestle, and analyzed with a Perkin-Elmer Model 240C Elemental Analyser. Instrument precision was determined by examining the variability obtained from replicate standards. Two independent subsamples of plant material were generally sufficient to replicate readings within less than 5 % difference. If readings were more variable, additional subsamples were analyzed. Samples collected in mid-July 1982 were combusted at 500°C for 10-12 hr to determine ash content.

Plant stands were also sampled for leaf area index (LAI), specific leaf area (SLA), and length of longest leaf during biomass sampling. Shoots were clipped below

the sediment surface, placed in seawater and brought to the lab. The first 20 healthy shoots were separated from the original sample as two subsamples of ten shoots each. The length of the longest leaf in each subsample was measured. Shoots in each subsample were sectioned in 10 cm intervals starting from the base of the leaf sheath. The leaf area (single side) of each progressive 10 cm section was determined using a Li-Cor Model 3100 Area Meter. Leaf area index (m^2 leaf surface [single side]$\cdot m^{-2}$ sediment surface) was calculated by multiplying the average leaf area per shoot by the shoot density per square meter determined from core samples taken on the same day, see above. SLA ($cm^2 \cdot g^{-1}$ dry wt leaf) was calculated by dividing the total leaf area of each 10-shoot subsample by its dry weight.

Leaf growth rates were measured using a hole punch technique (Zieman 1968). A leather punch fitted with a syringe needle was used to make a small hole at the base of each leaf. This method left an identifiable scar with minimal leaf damage. After 10-14 days, growth plots were sampled. In the lab, new growth was separated from the remainder of the shoot and dried at 60°C for 10-12 hr. Mean leaf growth (g dry wt$\cdot m^{-2} \cdot day^{-1}$) was calculated using density data obtained from core samples.

A Lambda incident light meter with LI-500 integrator was set up near the lagoon shore and recorded daily light levels throughout all sampling periods. Bottom-water temperatures were measured periodically using max-min thermometers placed in study plots for 10-14 days. Maximum temperatures were corelated by linear regression with maximum incident light readings from the same time periods.

Nitrogen uptake experiments using ^{15}N as a tracer were done in plexiglass chambers (McRoy and Goering 1974) between each clipping in 1982 and in April 1983. Each chamber was separated by a vertical and horizontal partition. The vertical divider was used to separate samples taken from clipped and control plots, while the horizontal separated shoots from roots-rhizomes. Plants were collected, rinsed of excess sediment in a screened box, and brought back to the lab in seawater. Individual shoots were separated with roots and rhizomes intact. Each shoot was placed in a single hole, rubber stopper and sealed with high vacuum silicone grease. The upper (shoot) portions of the chambers were filled with twice filtered (Gelman A/E glass fiber or Millipore 0.45 um filter) seawater. Leaves were entirely submerged. Care was taken that water did not leak from upper into lower

(root-rhizome) compartments of the chambers. Lower compartments were filled (1.75 l) with 60 or 300 uM NH_4Cl + $^{15}NH_4Cl$ in filtered seawater. Tracer (^{15}N) concentrations were 10% of final nitrogen concentrations. KH_2PO_4 (50 uM) was added to all root-rhizome compartments to assure that low phosphate concentration did not limit nitrogen uptake.

An individual uptake experiment consisted of 6 control shoots with roots-rhizomes (3 replicates in 60, and 3 in 300 uM NH_4Cl), and 6 clipped shoots with roots-rhizomes. Each experiment used plants from one station. Shoot compartments were aerated and chambers were placed outside for the duration of the experiment (24 hr) to simulate ambient conditions. After 24 hr, shoots and roots-rhizomes were removed from chambers, rinsed in deionized water, and separated into roots-rhizomes and leaves. Samples were dried at 60°C for 24-48 hr and shipped to Fairbanks for analysis.

In Fairbanks, samples were redried at 60°C for 12 hr, combusted with cuprox in a Coleman Nitrogen Analyzer, and analyzed for ^{15}N with a Jasco ^{15}N analyzer (Short 1981). Data from the Jasco passed directly to an HP85 computer that was programmed to calculate atom $\%^{15}N$ from measurements of $^{15}N_2$, $^{15}N + {}^{14}N$, and $^{14}N_2$. Readings were

calibrated with a standard curve generated from six individual standards (Sambrotto 1983). Uptake was calculated (uM N·uM N^{-1}·day^{-1}) after the method of Dugdale and Goering (1967).

Statistics were calculated using two-way ANOVA's with multiple observations (Steel and Torrie 1980). The design was randomized complete block. Sampling dates (seasonal effect) were defined as blocks; years (inter-annual effect) or clipped and control samples as treatments. The linear model for this analysis partitions components as elements due to mean, block, treatment, experimental error, and sampling error. The F statistic was calculated using the experimental error mean square. F statistics with $P<0.05$ were considered significant for both treatment and block effects. Means were plotted against standard deviations for all populations and examined for skewness and linearity. Similarity of variance was tested using the Hartley test (Neter and Wasserman 1974). Variances among root-rhizome biomass samples were not equal (probability of a type I error <0.01) and plots indicated a positive linear relationship between means and standard deviations. Consequently root-rhizome biomass data were log transformed for ANOVA.

RESULTS

Two different temporal trends in the data, as well as effects due to clipping were observed from analysis of variance (ANOVA). Significant inter-annual variations resulted from different environmental conditions or changes in the response of the plants to clipping between years. Seasonal effects reflected a pronounced pattern of response through the growing season common to both years (e.g., a comparison of clipping in 1981 with clipping in 1982) or within a given year due to particular environmental conditions (e.g., a comparison of clipped and control plants in 1981). Comparisons for which years were pooled did not yield information about seasonal effects. Means, standard deviations, and replicate samples are listed in Appendices 1 and 2 for Stations 2 and 8, respectively.

Four general results summarize clipping experiments. 1) Clipping produced significant differences at one or both stations for all parameters examined, with the exception of plant nitrogen content. 2) Clipping was more likely to cause a significant deviation from control patterns at Station 2 (shallow water, high root-rhizome to leaf ratio) than at Station 8 (deep water, low

root-rhizome to leaf ratio). 3) Clipping did not cause one station to resemble the other. Significant differences observed between control plots at Stations 2 and 8 were also significant for clipped plots. 4) Effects due to clipping were superimposed upon inter-annual variation. This last complication was particularly evident at Station 2 where clipping produced a significant difference in one year but not in the other.

Leaf Biomass

Significant differences between clipped and control plots at both stations indicated that plants were not regrowing completely between clips. Because there were no inter-annual differences at Station 2 ($P > 0.05$), leaf biomass samples from 1981 and 1982 were pooled and comparisons between clipped and control plants were made (Table 1). There was a highly significant difference in leaf biomass between clipped and control plants. Mean leaf biomass of plants from control plots was 143 g dry wt$\cdot m^{-2}$, while mean leaf biomass of clipped plants was 86 g dry wt$\cdot m^{-2}$ (Fig. 3). Clipped leaf biomass averaged 59 % of leaf biomass of control plants.

Leaf biomass data from Station 8 were somewhat more variable than those from Station 2, but inter-annual

Table 1. Results of two-way ANOVA of leaf biomass. Data were blocked by sampling date (seasonal effect). Levels of significance: $P<0.05$ (*), $P<0.01$ (**).

Study plot and source of variation	d.f.	F
Station 2:control		
Inter-annual effect	1	4.10
Seasonal effect	5	0.84
Station 2:clip		
Inter-annual effect	1	4.89
Seasonal effect	4	1.07
Station 2:pooled years		
Clipping effect	1	112.39**
Station 8:control		
Inter-annual effect	1	1.14
Seasonal effect	5	1.13
Station 8:clip		
Inter-annual effect	1	0.77
Seasonal effect	4	6.80*
Station 8:pooled years		
Clipping effect	1	211.91**
Control plants:pooled years		
Station effect	1	195.31**
Clipped plants:pooled years		
Station effect	1	6.34*

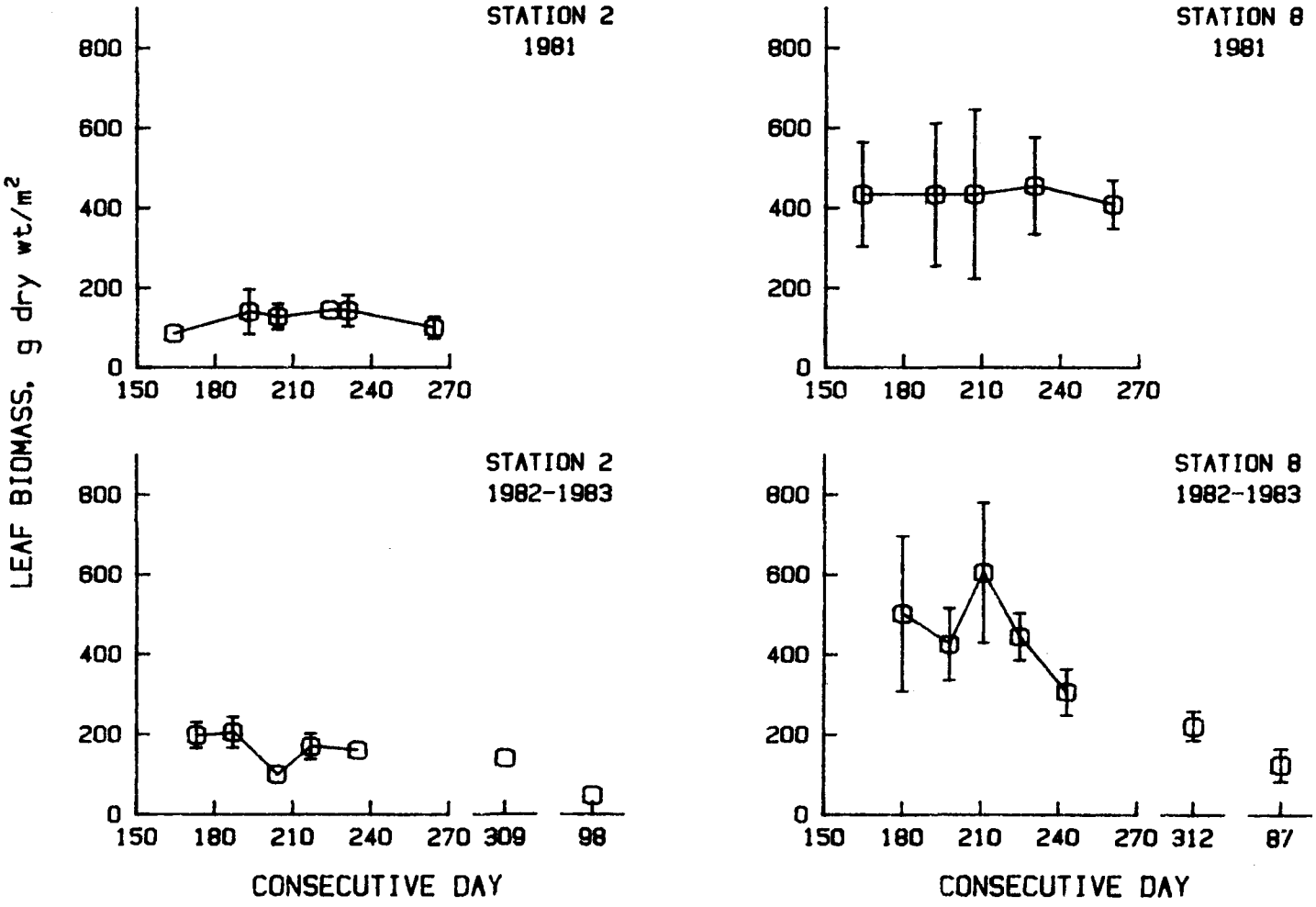

Fig. 3. Leaf biomass (g dry wt m^{-2}) in control plots at Stations 2 and 8, 1981-1983. Data are means +/- 1 s.d., n=5 for all samples. Day number 152 is June 1.

effects were similar. There was no significant inter-annual variability in leaf biomass of either clipped or control plants; there was, however, a significant seasonal effect in clipped but not in control plants. Pooled samples yielded a highly significant difference between clipped and control leaf biomass (Table 1). Mean biomass of clipped leaves was 132 g dry wt·m^{-2}, an average of 29 % of control leaf biomass (430 g dry wt·m^{-2}).

Leaf biomass at Station 2 was significantly lower than that at Station 8 in both clipped and control plots. However, clipping stress, as measured by relative loss of leaf biomass, was more severe at Station 8. The percent of control leaf biomass remaining after clipping was significantly lower at Station 8 (29 %) than at Station 2 (59 %).

Shoot Density

Shoot densities (number of vegetative shoots·m^{-2}) did not vary significantly between 1981 and 1982 for either clipped or control plants at Station 2 (Table 2). Consistent densities indicate a balance between shoot initiation and shoot mortality. Comparison of clipped and control shoot densities from pooled data (1981 and 1982), introduced a significant difference due to season that was

Table 2. Results of two-way ANOVA of shoot density. Data were blocked by sampling date (seasonal effect). Levels of significance: $P<0.05$ (*), $P<0.01$ (**).

Study plot and source of variation	d.f.	F
Station 2:control		
Inter-annual effect	1	0.70
Seasonal effect	5	1.69
Station 2:clip		
Inter-annual effect	1	0.04
Seasonal effect	4	0.95
Station 2:1981		
Clipping effect	1	8.87*
Seasonal effect	4	32.14**
Station 2:1982		
Clipping effect	1	1.51
Seasonal effect	4	1.68
Station 2:pooled years		
Clipping effect	1	0.76
Station 8:control		
Inter-annual effect	1	29.44**
Seasonal effect	5	2.09
Station 8:clip		
Inter-annual effect	1	9.25*
Seasonal effect	4	0.23
Station 8:1981		
Clipping effect	1	1.26
Seasonal effect	4	2.85
Station 8:1982		
Clipping effect	1	0.72
Seasonal effect	4	0.40
Control plants:1981		
Station effect	1	19.73**
Seasonal effect	5	1.18

Table 2. cont.

Study plot and source of variation	d.f.	F
Control plants:1982		
Station effect	1	80.00**
Seasonal effect	5	4.56
Clipped plants:1981		
Station effect	1	21.16**
Seasonal effect	4	2.11
Clipped plants:1982		
Station effect	1	45.14**
Seasonal effect	4	0.91

not present when either clipped or control plants were compared for inter-annual differences. Examination of the data indicated that the seasonal effect may have been the result of different patterns between years (Table 3). At both clipped and control plots densities rose steadily through the summer of 1981, while in 1982 densities were generally constant.

There were significant differences at Station 2 due to both seasonal effect and clipping in 1981; clipped plants occurred in consistently lower densities (mean = 7449 shoots$\cdot m^{-2}$) than did control plants (8220 shoots$\cdot m^{-2}$). In 1982, for which neither season nor clipping was significant, the clipped plot had consistently higher shoot densities (7720 shoots$\cdot m^{-2}$) than the control plot (7201 shoots$\cdot m^{-2}$).

Both clipped (4429) and control (4342) plots at Station 8 had significantly higher shoot densities in 1982 than in 1981 (2706 and 2463 shoots$\cdot m^{-2}$, respectively; Table 2). There were no differences due to clipping in either year, shoot densities were generally constant throughout the summer.

In both control and clipped plants there were significant differences in shoot densities between the two stations. Plants at Station 2 occurred in higher densities

Table 3. Shoot densities (shoots $\cdot m^{-2}$) from Stations 2 and 8. Data are means of five samples for each date. Sampling dates are listed as 1981/1982; consecutive days are listed above for comparison with figures. March and April data are from 1983.

Station 2

	Date							
	164/173	193/187	204/204	224/217	231/235	264	309	98
Study plot	13/22 June	12/6 July	23/23 July	12/5 August	19/23 August	21 September	5 November	8 April
1981								
Control	5083	4029	6971	10771	10819	11648	-	-
s.d.	364	732	2415	1675	1291	3353	-	-
Clipped	-	3505	6133	9476	7619	10514	-	-
s.d.	-	364	1902	1522	2180	1931	-	-
1982								
Control	7590	6457	6286	7048	7333	-	8495	3645
s.d.	1300	460	1210	1507	2133	-	2650	941
Clipped	7724	7810	6829	7219	9190	-	7552	-
s.d.	1046	671	671	1433	1259	-	750	-

Station 8

	Date							
	164/180	192/198	207/211	222/225	230/243	260	312	87
Study plot	13/29 June	11/17 July	26/30 July	10/13 August	18/31 August	20 September	8 November	28 March
1981								
Control	2726	2133	2267	2714	2119	2819	-	-
s.d.	452	418	535	267	451	260	-	-
Clipped	-	2333	1943	2552	2786	3914	-	-
s.d.	-	666	336	287	822	1132	-	-
1982								
Control	6119	3562	3505	4257	3676	-	4935	3258
s.d.	1198	374	1216	377	795	-	613	581
Clipped	4686	4086	4552	5143	4848	-	3514	3484
s.d.	1496	1396	2147	1582	519	-	1030	787

throughout the study than did those at Station 8.

Leaf Canopy

Leaf canopy measurements included leaf area index (LAI), specific leaf area (SLA), and length of longest leaf. LAI (m^2 leaf surface [one side]$\cdot m^{-2}$ sediment surface) is a measure of photosynthetic area per unit of sediment area, while SLA (cm^2 leaf surface [one side]$\cdot g^{-1}$ dry wt leaf) represents leaf area per gram dry weight of leaf. Longest leaf measurements represent, in a very general sense, the maximum height of the leaf canopy. In the case of clipped plants, longest leaves are usually the youngest leaves, those that have grown most rapidly after clipping. As a result, the length of longest leaves in clipped plots can be very different from the average clipped leaf length. LAI and length of longest leaf were directly affected by clipping, whereas SLA essentially reflects changes in leaf thickness independent of leaf length or area. All samples for leaf canopy measurements were taken 10-14 days after clipping.

There was no inter-annual or seasonal difference in LAI of control plants at Station 2 (Table 4). Means ranged from 1.8 to 6.6 (Table 5). There was, however, a highly significant difference between years for clipped plants,

Table 4. Results of two-way ANOVA of leaf area index. Data were blocked by sampling date (seasonal effect). Levels of significance: $P<0.05$ (*), $P<0.01$ (**).

Study plot and source of variation	d.f.	F
Station 2:control		
Inter-annual effect	1	3.09
Seasonal effect	4	1.10
Station 2:clip		
Inter-annual effect	1	30.94*
Seasonal effect	3	0.14
Station 2:1981		
Clipping effect	1	11.49*
Seasonal effect	3	1.34
Station 2:1982		
Clipping effect	1	2.64
Seasonal effect	3	1.58
Station 2:pooled years		
Clipping effect	1	7.09*
Station 8:control		
Inter-annual effect	1	2.67
Seasonal effect	4	2.22
Station 8:clip		
Inter-annual effect	1	1.62
Seasonal effect	3	6.42
Station 8:pooled years		
Clipping effect	1	26.94**
Control plants:pooled years		
Station effect	1	58.81**
Clipped plants:1981		
Station effect	1	1.52
Seasonal effect	3	0.45
Clipped plants:1982		
Station effect	1	0.17
Seasonal effect	4	15.25*

Table 5. Leaf area index from Stations 2 and 8. Data are means of two subsamples of ten shoots each. Dates are listed as 1981/1982; Consecutive days are listed above for comparison with figures.

Station 2	Date					
	164/173	193/187	204/204	224/217	231/235	309
Study plot	13/22 June	12/6 July	23/23 July	12/5 August	19/23 August	5 November
1981						
Control	5.1	1.8	5.3	5.1	6.6	-
Clipped	-	1.2	1.4	1.8	1.5	-
1982						
Control	3.3	3.5	3.7	2.5	3.8	3.7
Clipped	-	3.2	3.1	2.7	2.6	1.1

Station 8	Date					
	164/180	192/198	207/211	222/225	230/243	312
Study plot	13/29 June	11/17 July	26/30 July	10/13 August	18/31 August	5 November
1981						
Control	10.1	6.1	11.6	7.1	11.1	-
Clipped	-	3.4	3.1	1.2	1.5	-
1982						
Control	6.6	7.7	6.4	4.5	10.9	3.0
Clipped	6.0	4.0	2.7	2.6	1.8	1.0

with plants having a greater LAI in 1982. LAI of clipped plants ranged from 1.2 to 3.3.

At Station 8 there was no inter-annual or seasonal difference for either clipped or control plants (Table 4). Clipped plants had significantly lower LAI than did control plants. The means of control and clipped plant LAI varied from 4.5 to 11.6 and 1.2 to 4.0, respectively (Table 5). There was a highly significant difference between control plants from Stations 2 and 8. Differences between clipped plants from the two stations were not significant indicating that photosynthetic area was the same at both stations after clipping.

Mean SLA of control plants at Station 2 was lower in 1981 (186 $cm^2 \cdot g^{-1}$) than in 1982 (243 $cm^2 \cdot g^{-1}$; Fig. 4). This difference represented a general pattern which was significant between years, there was no significant seasonal effect (Table 6). Clipped plants showed a similar trend but the difference between years was not significant, while seasonal effects were. SLA of clipped plants ranged from 151 to 254 $cm^2 \cdot g^{-1}$. The more pronounced increase in SLA of control plants in 1982 led to a significant difference between clipped and control plants that was not evident in 1981.

At Station 8, there was no significant seasonal

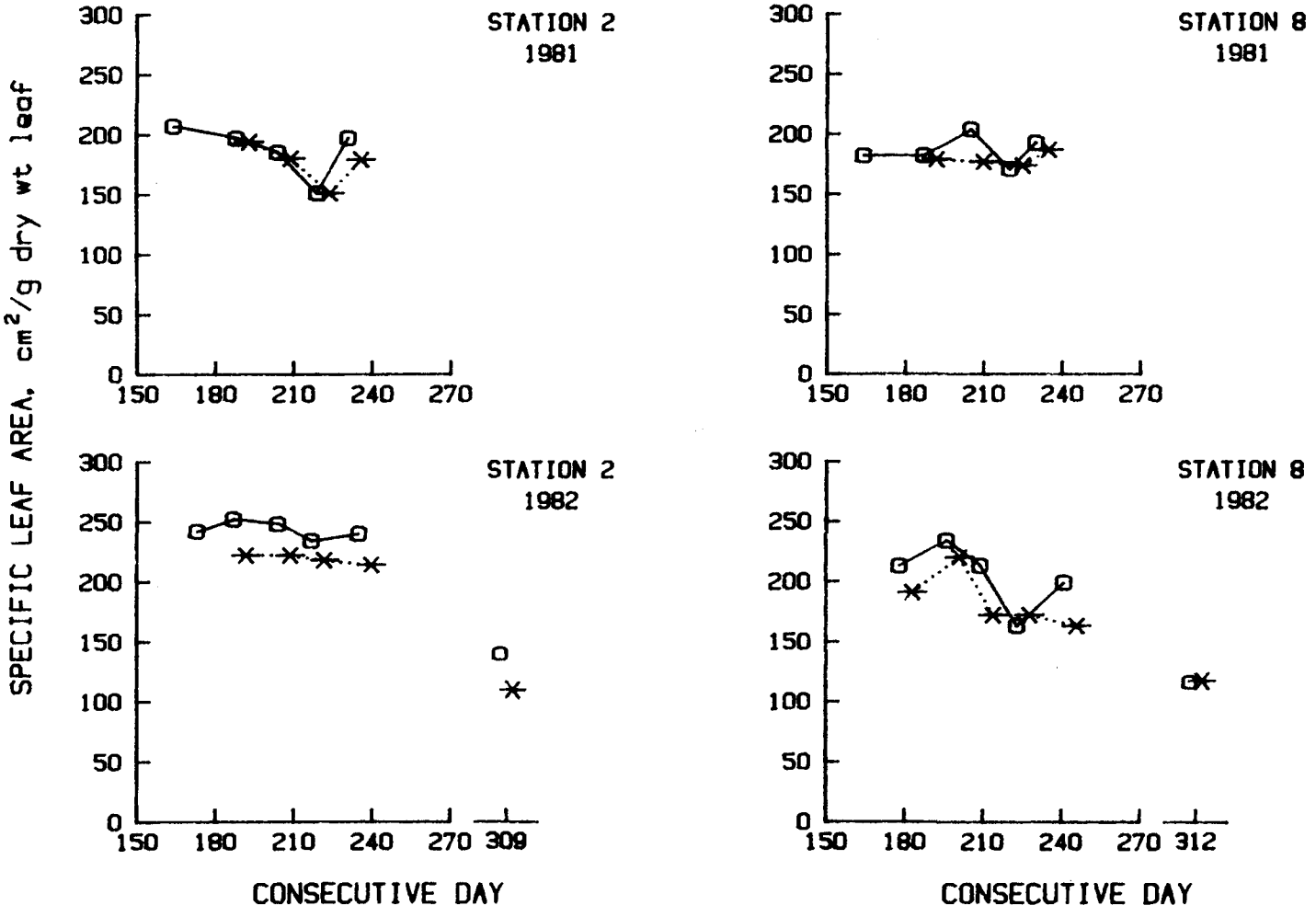

Fig. 4. Specific leaf area ($cm^2 \cdot g^{-1}$) in control (open circles) and clipped (asterisks) plots at Stations 2 and 8, 1981-1982. Data are calculated as the means of two subsamples of ten shoots each. Day number 152 is June 1.

effect or difference in SLA between 1981 and 1982 for clipped or control plants (Table 6). However, there was a trend toward higher SLA in 1982 as observed at Station 2 (Fig. 4). Mean SLA of control and clipped plants were 195 and 181 $cm^2 \cdot g^{-1}$ respectively. No comparisons between years or treatments were statistically significant.

Comparisons of control plants from Stations 2 and 8 indicated no difference between stations in 1981. Higher SLA in 1982 at Station 2 resulted in a significant difference between stations the second year of the study. There was no difference in SLA between clipped plants from Stations 2 and 8.

At Station 2 there were no significant inter-annual or seasonal differences in length of longest leaves from either control (mean = 34 cm) or clipped (21 cm) plots (Tables 7 and 8). Data were pooled for further comparison. There was a highly significant difference in length of longest leaves between clipped and control plots, indicating that the fastest growing leaves in the clipped plot did not equal the maximum canopy height in the control plot before the plot was re-clipped.

Longest leaves from control plots at Station 8 were not significantly different in length in 1981 (mean = 105 cm) and 1982 (74 cm). Clipped leaves, however, were

Table 6. Results of two-way ANOVA of specific leaf area. Data were blocked by sampling date (seasonal effect). Levels of significance: $P<0.05$ (*), $P<0.01$ (**).

Study plot and source of variation	d.f.	F
Station 2:control		
Inter-annual effect	1	65.42**
Seasonal effect	4	5.12
Station 2:clip		
Inter-annual effect	1	2.79
Seasonal effect	3	128.74**
Station 2:1981		
Clipping effect	1	2.36
Seasonal effect	3	23.25*
Station 2:1982		
Clipping effect	1	68.99**
Seasonal effect	3	3.57
Station 8:control		
Inter-annual effect	1	2.78
Seasonal effect	4	2.16
Station 8:clip		
Inter-annual effect	1	0.04
Seasonal effect	3	0.86
Station 8:pooled years		
Clipping effect	1	4.61
Control plants:1981		
Station effect	1	0.02
Seasonal effect	4	2.14
Control plants:1982		
Station effect	1	16.85*
Seasonal effect	4	2.24
Clipped Plants:pooled years		
Station effect	1	2.84

Table 7. Results of two-way ANOVA of length of longest leaves. Data were blocked by sampling date (seasonal effect). Levels of significance: $P<0.05$ (*), $P<0.01$ (**).

Study plot and source of variation	d.f.	F
Station 2:control		
Inter-annual effect	1	0.53
Seasonal effect	4	2.22
Station 2:clip		
Inter-annual effect	1	2.75
Seasonal effect	3	0.48
Station 2:pooled years		
Clipping effect	1	26.51**
Station 8:control		
Inter-annual effect	1	5.81
Seasonal effect	5	1.15
Station 8:clip		
Inter-annual effect	1	33.24*
Seasonal effect	3	47.30**
Station 8:1981		
Clipping effect	1	6.70
Seasonal effect	3	0.37
Station 8:1982		
Clipping effect	1	17.93*
Seasonal effect	4	1.59
Station 8:pooled years		
Clipping effect	1	20.58**
Control plants:pooled years		
Station effect	1	38.43
Clipped plants:1981		
Station effect	1	14.67*
Seasonal effect	3	0.63
Clipped plants:1982		
Station effect	1	6.70
Seasonal effect	3	5.09

Table 8. Length of longest leaves (cm) from Stations 2 and 8. Data are length of longest leaves from two subsamples of ten shoots each. Sampling dates are listed as 1981/1982; consecutive days are listed above for comparison with figures. March and April data are from 1983.

Station 2

	Date						
	164/173	193/187	204/204	224/217	231/235	309	98
Study plot	13/22 June	12/6 July	23/23 July	12/5 August	19/23 August	5 November	8 April
1981							
Control	30	22	45	27	38	-	-
	38	26	34	35	-	-	-
Clipped	-	17	14	14	28	-	-
	-	17	14	12	-	-	-
1982							
Control	30	36	41	34	46	35	13
	25	34	34	32	46	28	15
Clipped	-	29	33	23	22	16	-
	-	32	27	23	28	15	-

Station 8

	Date							
	164/180	192/198	207/211	222/225	230/243	260	312	87
Study plot	13/29 June	11/17 July	26/30 July	10/13 August	18/31 August	20 September	8 November	28 March
1981								
Control	95	62	94	97	147	127	-	-
	93	60	97	101	142	141	-	-
Clipped	-	55	47	36	37	-	-	-
	-	61	44	36	-	-	-	-
1982								
Control	51	84	90	61	93	-	54	36
	49	69	90	49	102	-	40	32
Clipped	46	48	35	32	22	-	22	13
	49	52	39	28	25	-	18	15

significantly longer after regrowth in 1981 (45 cm) than in 1982 (35 cm). There was also a seasonal effect in clipped plants that was not evident in control plants. As a result, the longest leaves from clipped plots were not significantly shorter than those from control plots in 1981. Lack of a statistically significant difference in 1981 was likely due to the small number of degrees of freedom from a single year's information, and the similarity between clipped and control data collected on 11 July. Control plants sampled on this date were unusually short compared with others from the same year, and clipped plants were unusually long. When data from 1981 were pooled with samples from 1982, there was a higher probability of difference between clipped and control leaves from both years than was calculated for the 1982 data alone. This indicated that samples collected in 1981 contributed to the significant difference in longest leaves between clipped and control plots.

The length of longest leaves from control plots were significantly longer at Station 8 than at Station 2. Longest leaves from clipped plots were consistently longer at Station 8 than those at Station 2, but this difference was only significant in 1981 due to the general increase in leaf length from 1981 to 1982 in the clipped plot at

Station 2. At Station 2, increased leaf length and LAI in clipped plots in the second year of the study may be the result of differences in clipping technique between years or faster leaf regrowth in 1982.

Root-Rhizome Biomass

Mean root-rhizome biomass from control plots at Station 2 was 435 g dry wt·m^{-2} (Fig. 5). There were no significant inter-annual differences or seasonal effects (Table 9). Biomass of clipped plants however, was significantly greater in 1982 (462 g dry wt·m^{-2}) than in 1981 (303 g dry wt·m^{-2}). Clipped plants had significantly lower root-rhizome biomass in 1981 than control plants; there was no significant difference in 1982. There was a significant seasonal effect in all comparisons of clipped and control plants; biomass was highest in spring and fall and lowest in mid-summer.

At Station 8, there was no difference between years in root-rhizome biomass from control plots (mean = 617 g dry wt·m^{-2}), but clipped plants had significantly higher biomass in 1982 (729) than in 1981 (462; Fig. 5; Table 9). There was no significant difference due to clipping for either year. Seasonal effects were significant in comparisons of clipped and control plants in 1981 but not

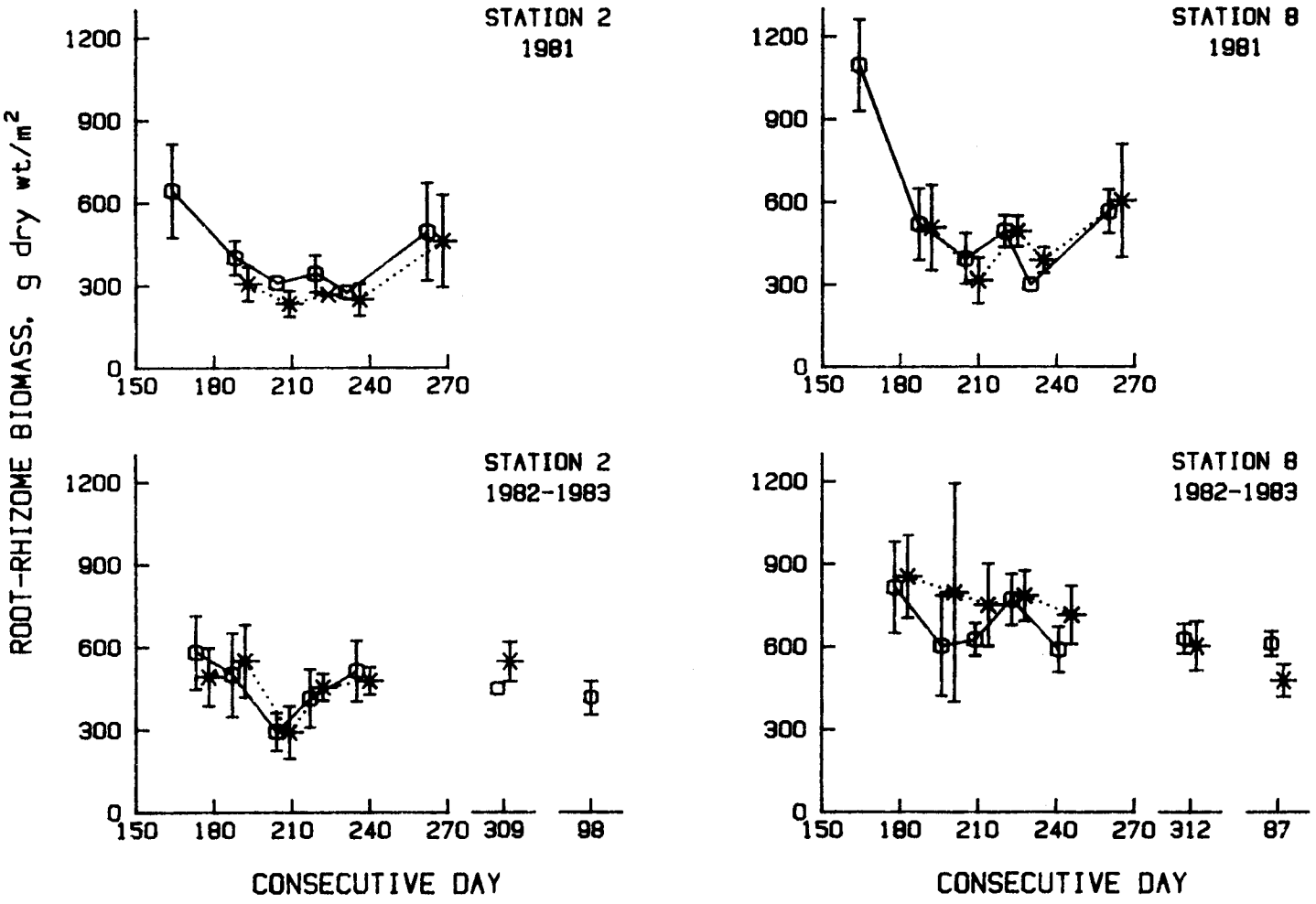

Fig. 5. Root-rhizome biomass (g dry wt·m^{-2}) in control (open circles) and clipped (asterisks) plots at Stations 2 and 8, 1981-1983. Data are means +/- 1 s.d., n=5 for all samples. Day number 152 is June 1.

Table 9. Results of two-way ANOVA of log transformations of root-rhizome biomass. Data were blocked by sampling date (seasonal effect). Levels of significance: $P<0.05$ (*), $P<0.01$ (**).

Study plot and source of variation	d.f.	F
Station 2:control		
Inter-annual effect	1	1.30
Seasonal effect	5	3.08
Station 2:clip		
Inter-annual effect	1	20.18*
Seasonal effect	4	4.93
Station 2:1981		
Clipping effect	1	21.27**
Seasonal effect	4	22.51**
Station 2:1982		
Clipping effect	1	1.81
Seasonal effect	4	19.08**
Station 8:control		
Inter-annual effect	1	3.17
Seasonal effect	5	2.49
Station 8:clip		
Inter-annual effect	1	12.06*
Seasonal effect	4	0.49
Station 8:1981		
Clipping effect	1	0.02
Seasonal effect	4	7.03*
Station 8:1982		
Clipping effect	1	4.63
Seasonal effect	4	2.24
Control plants:pooled years		
Station effect	1	30.43**

Table 9. cont.

Study plot and source of variation	d.f.	F
Clipped plants: 1981		
Station effect	1	44.29**
Seasonal effect	4	11.47*
Clipped plants: 1982		
Station effect	1	9.68*
Seasonal effect	4	0.56

in 1982. A combination of changes in overall mean biomass from 1981 to 1982, and lack of a significant seasonal effect in 1982, indicated that the seasonal pattern in biomass in clipped plots had changed from the first to second year of the study (Fig. 5).

Control plants at Station 8 had significantly higher root-rhizome biomass throughout the study than did plants at Station 2. In both years, clipped plants had significantly higher root-rhizome biomass at Station 8 than at Station 2.

Carbon and Nitrogen Content

All carbon and nitrogen concentrations (% of ash free dry wt) were corrected for ash content (Table 10). Roots only, without rhizomes, were analyzed for carbon and nitrogen concentration.

Comparisons of carbon contents of old and new leaves at Station 2 indicated no significant difference due to leaf age in either plot (Table 11). Data from old and new leaves were pooled, mean carbon content was 47.9 % in control and 49.6% in clipped plots. Clipped leaves had significantly higher carbon concentrations than did control leaves. The difference was particularly obvious late in summer when clipped leaves averaged 50.2 % and

Table 10. Ash content (% dry wt) of leaves and roots sampled in mid-July 1982. Data are independent subsamples of freeze dried leaves and roots.

Study plot	New leaves	Old leaves	Roots
Station 2			
Control	17%	17%	21%
		17%	21%
Clip	21%	21%	20%
		21%	23%
Station 8			
Control	16%	17%	19%
		17%	20%
Clip	16%	21%	18%
		20%	20%

Table 11. Results of two-way ANOVA of carbon content in leaves. Data were blocked by sampling date (seasonal effect). Levels of significance: $P<0.05$ (*), $P<0.01$ (**).

Study plot and source of variation	d.f.	F
Station 2:control		
Leaf age effect	1	0.02
Seasonal effect	4	6.32
Station 2:clip		
Leaf age effect	1	1.03
Seasonal effect	4	32.80**
Station 2:pooled leaves		
Clipping effect	1	10.69**
Station 8:control		
Leaf age effect	1	2.51
Seasonal effect	4	7.45*
Station 8:clip		
Leaf age effect	1	1.03
Seasonal effect	3	1.99
Station 8:pooled leaves		
Clipping effect	1	1.06
Control plants:pooled leaves		
Station effect	1	18.96**
Clipped plants:pooled leaves		
Station effect	1	14.13**

control leaves averaged 47.4 % carbon (Fig. 6).

There were no significant differences between leaf ages or treatments at Station 8 (Table 11). Old and new leaves averaged 46.5 % C in control plots and 47.2 % C in clipped plots (Fig. 6).

For comparisons between stations, old and new leaf data were pooled. Both clipped and control leaves from Station 2 had significantly higher carbon concentrations than did respective samples from Station 8.

Carbon concentrations of root samples from clipped and control plots were not significantly different (Table 12) for either Station 2 (means = 43.8 and 44.3 %, respectively) or 8 (43.6 and 43.8 %). Pooled data of roots from clipped and control plots showed that carbon concentrations were similar at both stations. Because patterns of carbon concentration were quite different in clipped and control plots, and few degrees of freedom were available for comparison of clipped and control plots at any one station, data from both stations were pooled. A comparison of clipped and control plants revealed significantly lower carbon concentrations in roots of clipped plants.

There were no significant differences in nitrogen concentrations for any comparison at either station or

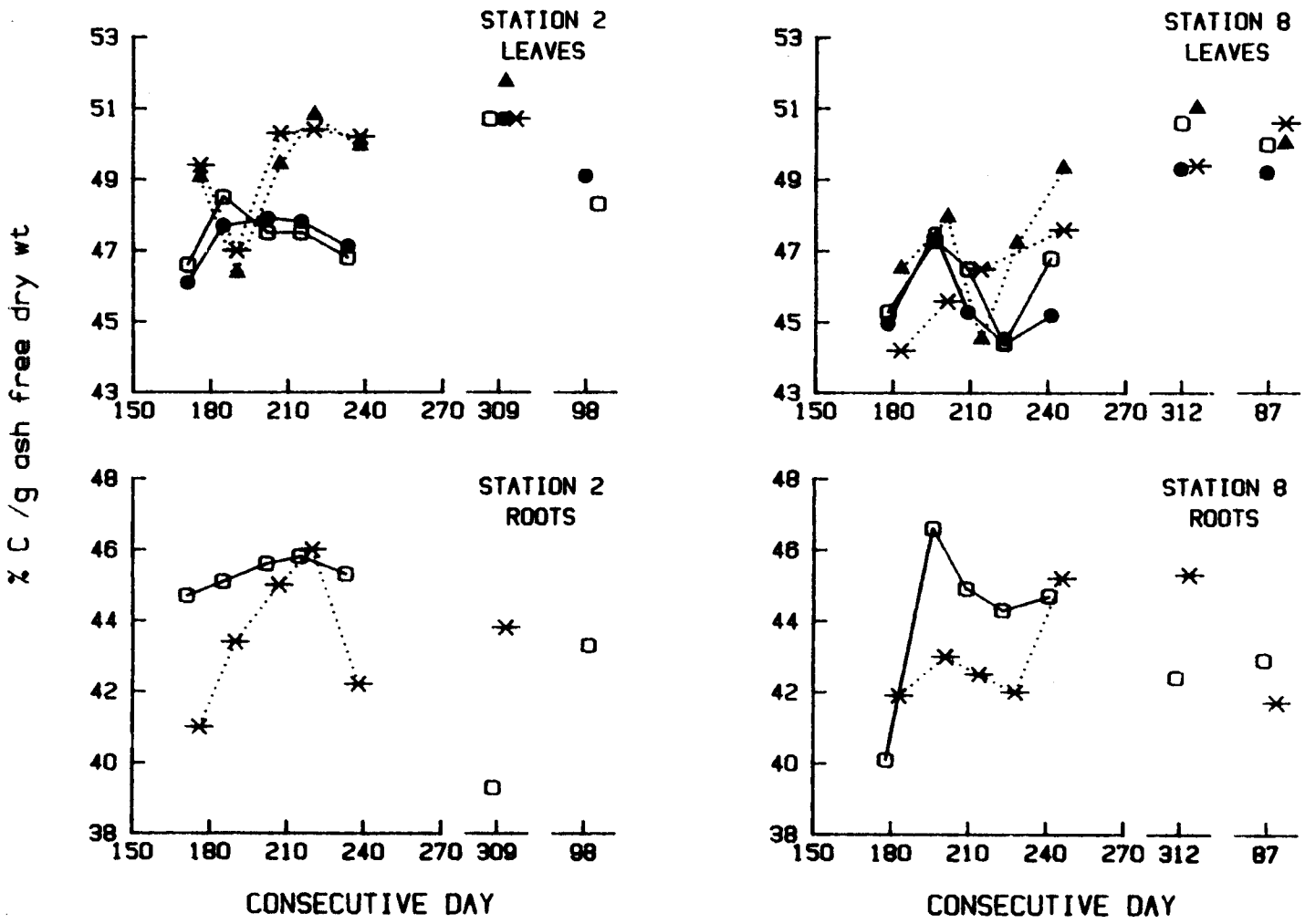

Fig. 6. Carbon content (% of ash free dry wt) from control and clipped plots at Stations 2 and 8, 1982-1983. Upper panels: new leaves, control (open circles); old leaves, control (solid circles); new leaves, clipped (asterisks); and old leaves, clipped (solid triangles). Lower panels: roots, control (open circles) and clipped (asterisks). Data are means of two, independent subsamples.

Table 12. Results of two-way ANOVA of carbon content of roots. Data were blocked by sampling date (seasonal effect). Levels of significance: $P<0.05$ (*), $P<0.01$ (**).

Study plot and source of variation	d.f.	F
Station 2		
Clipping effect	1	6.29
Seasonal effect	4	2.43
Station 8		
Clipping effect	1	1.18
Seasonal effect	4	2.12
Pooled:clipped and control		
Station effect	1	1.61
Pooled:pooled stations		
Clipping effect	1	5.85*

between stations, with the exception of a significant difference due to leaf age (Tables 13 and 14). Mean nitrogen content of new and old leaves was 2.4 % and 1.4 %, respectively at Station 2, and 2.4 % and 1.8 % at Station 8. New leaves had significantly higher nitrogen content than old leaves at both stations (Fig. 7). Nitrogen content in leaves in March and April approximately doubled with respect to summer samples. New leaves averaged 5.3 % and old leaves averaged 4.1 %. High nitrogen content in leaves probably resulted from high concentrations in the water column. *Zostera marina* in Izembek Lagoon has been shown to take up nitrogen through leaves as well as roots (Short and McRoy 1984). Root concentrations of nitrogen were relatively constant through summer and spring, the overall mean was 1.3 %.

Leaf Growth

Leaf growth rates were calculated as both areal (g dry wt $\cdot m^{-2} \cdot day^{-1}$) and individual shoot (mg dry wt $\cdot shoot^{-1} \cdot day^{-1}$) rates (Table 15). Because leaf growth data were collected at different times at the two stations, comparisons are qualitative.

Leaf growth rates per unit area in control plots at Station 2 were generally highest early in summer

Table 13. Results of two-way ANOVA of nitrogen content in leaves. Data were blocked by sampling date (seasonal effect). Levels of significance: $P<0.05$ (*), $P<0.01$ (**).

Study plot and source of variation	d.f.	F
Station 2:control		
Leaf age effect	1	147.78**
Seasonal effect	5	17.63**
Station 2:clip		
Leaf age effect	1	104.97**
Seasonal effect	5	3.41
Station 2:new leaves		
Clipping effect	1	1.79
Seasonal effect	5	1.76
Station 2:old leaves		
Clipping effect	1	5.76
Seasonal effect	5	1.95
Station 8:control		
Leaf age effect	1	118.72**
Seasonal effect	5	18.98**
Station 8:clip		
Leaf age effect	1	58.34**
Seasonal effect	4	11.48*
Station 8:new leaves		
Clipping effect	1	0.72
Seasonal effect	4	1.31
Station 8:old leaves		
Clipping effect	1	0.77
Seasonal effect	5	3.39
New leaves:clipped and control		
Station effect	1	0.08
Old leaves:clipped and control		
Station effect	1	1.97

Table 14. Results of two-way ANOVA of nitrogen content in roots. Data were blocked by sampling date (seasonal effect). Levels of significance: $P<0.05$ (*), $P<0.01$ (**).

Study plot and source of variation	d.f.	F
Station 2		
Clipping effect	1	<0.01
Seasonal effect	5	0.17
Station 8		
Clipping effect	1	1.89
Seasonal effect	5	1.66
Pooled:clipped and control		
Station effect	1	1.13
Pooled:pooled stations		
Clipping effect	1	0.31

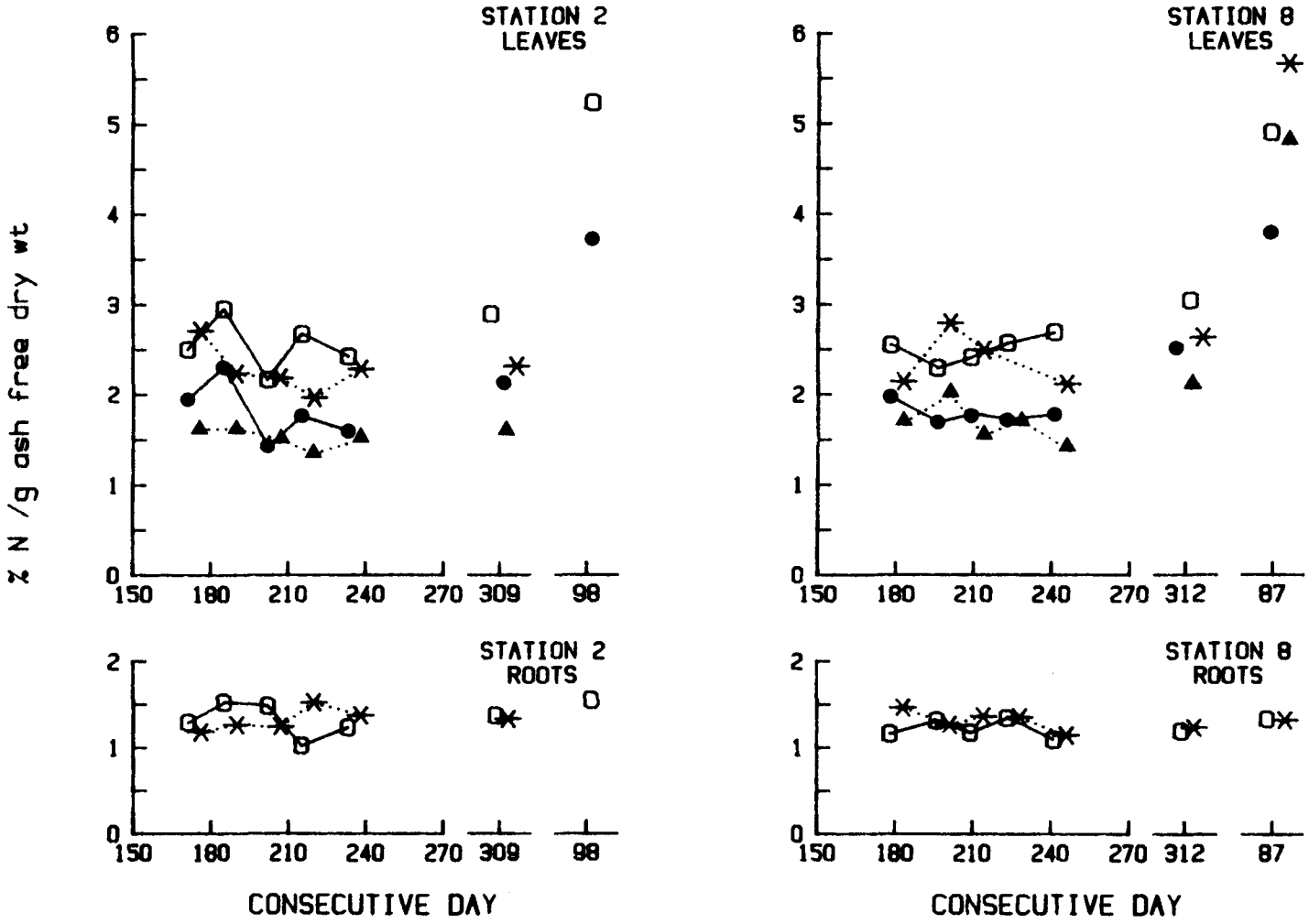

Fig. 7. Nitrogen content (% of ash free dry wt) from control and clipped plots at Stations 2 and 8, 1982-1983. Upper panels: new leaves, control (open circles); old leaves, control (solid circles); new leaves, clipped (asterisks); and old leaves, clipped (solid triangles). Lower panels: roots, control (open circles) and clipped (asterisks). Data are means of two, independent subsamples.

Table 15. Leaf growth rates calculated as areal rates (g dry wt $\cdot m^{-2} \cdot day^{-1}$) and individual rates (mg dry wt $\cdot shoot^{-1} \cdot day^{-1}$) for Stations 2 and 8. Rates were calculated from means of new leaf growth, sample numbers ranged from 3 to 18 at Station 2 and 3 to 38 at Station 8. Sampling dates are listed as 1981/1982; consecutive days are listed above for comparison with figures. April data are from 1983.

	Date							
	160/ 158	202/ 194	210/ 209	216/ 219	232/ 231	249	322	309
	9/7 June	21/13 July	29/28 July	4/7 August	19/18 August	7 September	18 November	5 April
Areal:1981								
Station 2								
Control	-	6.8	26.8	-	7.7	-	-	-
Clipped	-	3.1	7.6	-	0.8	-	-	-
Station 8								
Control	7.1	8.4	-	3.9	2.7	-	-	-
Clipped	2.9	3.5	-	3.5	1.2	-	-	-
Areal:1982								
Station 2								
Control	23.5	-	-	-	-	2.2	-	1.0
Clipped	12.0	-	-	2.7	-	2.0	-	-
Station 8								
Control	-	15.9	5.7	-	6.3	3.4	1.4	2.1
Clipped	-	4.8	2.4	-	3.3	1.4	1.1	1.3
Individual:1981								
Station 2								
Control	-	977	2483	-	519	-	-	-
Clipped	-	504	804	-	110	-	-	-
Station 8								
Control	3323	3724	-	1433	1251	-	-	-
Clipped	1256	1776	-	1356	445	-	-	-
Individual:1982								
Station 2								
Control	3639	-	-	-	-	300	-	274
Clipped	1536	-	-	374	-	218	-	-
Station 8								
Control	-	4464	1626	-	1480	925	284	645
Clipped	-	1175	527	-	642	289	313	373

(>20 g dry wt·m^{-2}·day^{-1}), although plants were apparently able to take advantage of favorable conditions through mid-summer (see data from 29 July 1981, Table 15). Plants in control plots had consistently higher leaf growth rates (both areal and individual) than did clipped plants. Patterns of leaf growth at Station 8 were similar to those at Station 2.

Growth rates of individual shoots at Station 2 were generally lower than were those at Station 8. Mean growth rates of control shoots from comparable sampling dates were 1365 and 2074 mg dry wt·$shoot^{-1}$·day^{-1} at Stations 2 and 8, respectively. When calculated on an areal basis, however, higher shoot densities at Station 2 than at Station 8, resulted in similar rates of leaf growth per unit area for control plants. In general, areal growth rates from clipped plots were similar for both stations, except mid-summer 1981 and early summer 1982 when leaf growth was considerably faster at Station 2.

Nitrogen Uptake

Calculations from ^{15}N tracer experiments of plant nitrogen uptake (uM N·uM N^{-1}·day^{-1}; Dugdale and Goering 1967) indicated that plants from control plots sampled in summer did not allocate measurable quantities of nitrogen

to leaves during the course of the experiment (Table 16). However, plants from clipped plots, especially those from Station 2, did exhibit translocation of ^{15}N from the roots to the leaves. Comparisons of clipped plants and those from early spring, suggested that clipping and initial shoot growth at the onset of the growing season produced a similar nitrogen demand in leaves.

Because allocation to leaves was increased by clipping, calculations of nitrogen uptake by roots from final ^{15}N content likely underestimated total uptake by roots of clipped plants. Comparisons of clipped and control plants indicated no significant clipping effect on root nitrogen uptake at either station (Table 17). Lack of a significant difference suggests that total root nitrogen uptake of clipped plants was greater than that of control plants because of allocation to leaves in clipped plants. However, few degrees of freedom and fairly large variability among experiments (Table 18) make this conclusion tenuous.

There were significant differences in uptake due to initial concentrations. Plants from Station 2 had significantly greater nitrogen uptake rates in high-nitrogen (300 uM NH_4Cl) than in low-nitrogen (60 uM NH_4Cl) experiments. Uptake rates from high-nitrogen

Table 16. Nitrogen translocation (uM N·uM N^{-1}·day^{-1}) to leaves from roots from Stations 2 and 8. Data are means (n=3) from low-nitrogen (60 uM NH_4Cl) and high-nitrogen (300 uM NH_4Cl) experiments. Dates are listed for experiments from Station 2/Station 8 in 1982; consecutive days are listed above for comparison with figures. April data are from 1983.

	Date					
Experiment	195/- 14/- July	211/204 30/23 July	214/209 2/29 August/ July	228/223 16/11 August	231/235 19/23 August	100/102 10/12 April
Low-nitrogen						
Station 2						
Control	0.01	<0.01	<0.01	<0.01	<0.01	0.03
Clipped	0.05	0.01	0.02	0.01	0.01	-
Station 8						
Control	-	<0.01	<0.01	<0.01	<0.01	0.02
Clipped	-	0.02	<0.01	<0.01	0.01	0.01
High-nitrogen						
Station 2						
Control	<0.01	<0.01	<0.01	<0.01	<0.01	0.02
Clipped	0.02	<0.01	0.01	0.03	0.01	-
Station 8						
Control	-	<0.01	<0.01	<0.01	<0.01	0.03
Clipped	-	<0.01	0.01	<0.01	0.01	0.03

Table 17. Results of two-way ANOVA of ^{15}N uptake by roots from low-nitrogen (60uM NH_4Cl) and high-nitrogen (300uM NH_4Cl) uptake experiments. Data were blocked by sampling date (seasonal effect). Levels of significance: $P<0.05$ (*), $P<0.01$ (**).

Study plot and source of variation	d.f.	F
Station 2:control		
Concentration effect	1	3.83
Seasonal effect	3	0.60
Station 2:clip		
Concentration effect	1	2.78
Seasonal effect	3	0.04
Station 2:pooled concentrations		
Clipping effect	1	1.58
Station 2:low concentration		
Clipping effect	1	0.57
Seasonal effect	3	0.63
Station 2:high concentration		
Clipping effect	1	0.84
Seasonal effect	3	0.43
Station 2:clipped and control		
Concentration effect	1	7.54*
Station 8:control		
Concentration effect	1	3.95
Seasonal effect	3	1.78
Station 8:clip		
Concentration effect	1	0.75
Seasonal effect	3	6.08
Station 8:pooled concentrations		
Clipping effect	1	1.07
Low concentration:clip and control		
Station effect	1	3.40
High concentration:clip and control		
Station effect	1	16.81**

Table 18. Nitrogen uptake (uM N·uM N^{-1}·day^{-1}) by roots from Stations 2 and 8. Data are means (n=3) from low-nitrogen (60 uM NH_4Cl) and high-nitrogen (300 uM NH_4Cl) experiments. Dates are listed for experiments from Station 2/Station 8 in 1982; consecutive days are listed for comparison with figures. April data are from 1983.

	Date					
Experiment	195/- 14/- July	211/204 30/23 July	214/209 2/29 August/ July	228/223 16/11 August	231/235 19/23 August	100/102 10/12 April
Low-nitrogen						
Station 2						
Control	0.10	0.21	0.21	0.12	0.13	0.08
Clipped	0.11	0.09	0.15	0.10	0.21	-
Station 8						
Control	-	0.06	0.08	0.11	0.12	0.14
Clipped	-	0.04	0.13	0.16	0.17	0.12
High-nitrogen						
Station 2						
Control	0.17	0.27	0.23	0.22	0.43	0.09
Clipped	0.12	0.29	0.18	0.26	0.18	-
Station 8						
Control	-	0.17	0.07	0.14	0.20	0.10
Clipped	-	0.10	0.09	0.18	0.20	0.12

experiments at Station 2 were also significantly greater than rates calculated at Station 8 under the same initial concentrations.

Light and Temperature

Because this study was conducted through two years, and inter-annual effects were often significant, changes in environmental variables were considered. Continuous bottom-water temperature measurements were not made in Izembek Lagoon, consequently, the relationship between discrete maximum temperatures (Table 19) and incident light levels (Appendix 3) was used to examine changes in weather conditions. There was a significant positive reationship between maximum water temperature and maximum incident light (Fig. 8). This relationship was used to estimate the number of days in each year that bottom-water temperatures were warm enough, i.e., 20°C, to effectively increase net photosynthesis (Biebl and McRoy 1971, Drew 1979). Because the light meter recorded integrated values, day length as well as cloud cover affected incident light readings. Consequently, comparisons between 1981 and 1982 included the period between 19 June and 22 August when data were available for both years. In 1982 there were 13 days during which water temperatures likely reached or

Table 19. Maximum and minimum bottom-water temperatures (°C) at study plots in Izembek Lagoon, 1981-1983.

Date	Station-study plot	Water temperature	
		Maximum	Minimum
8 July 1981	2-Control	24	11
9 July 1981	8-Control	21	11
26 July 1981	2-Clip	24	11
14 August 1981	2-Clip	19	10
	8-Control	18	11
2 August 1982	8-Control	-	9
	8-Clip	-	10
21 August 1982	2-Control	19	11
	2-Clip	23	8
3 September 1982	2-Control	15	8
	2-Clip	17	9
14 November 1982	2-Clip	7	1
18 November 1982	2-Control	8	2
	2-Clip	8	3
5 April 1983	2-Control	20	6
6 April 1983	8-Control	12	2
16 April 1983	8-Control	22	8

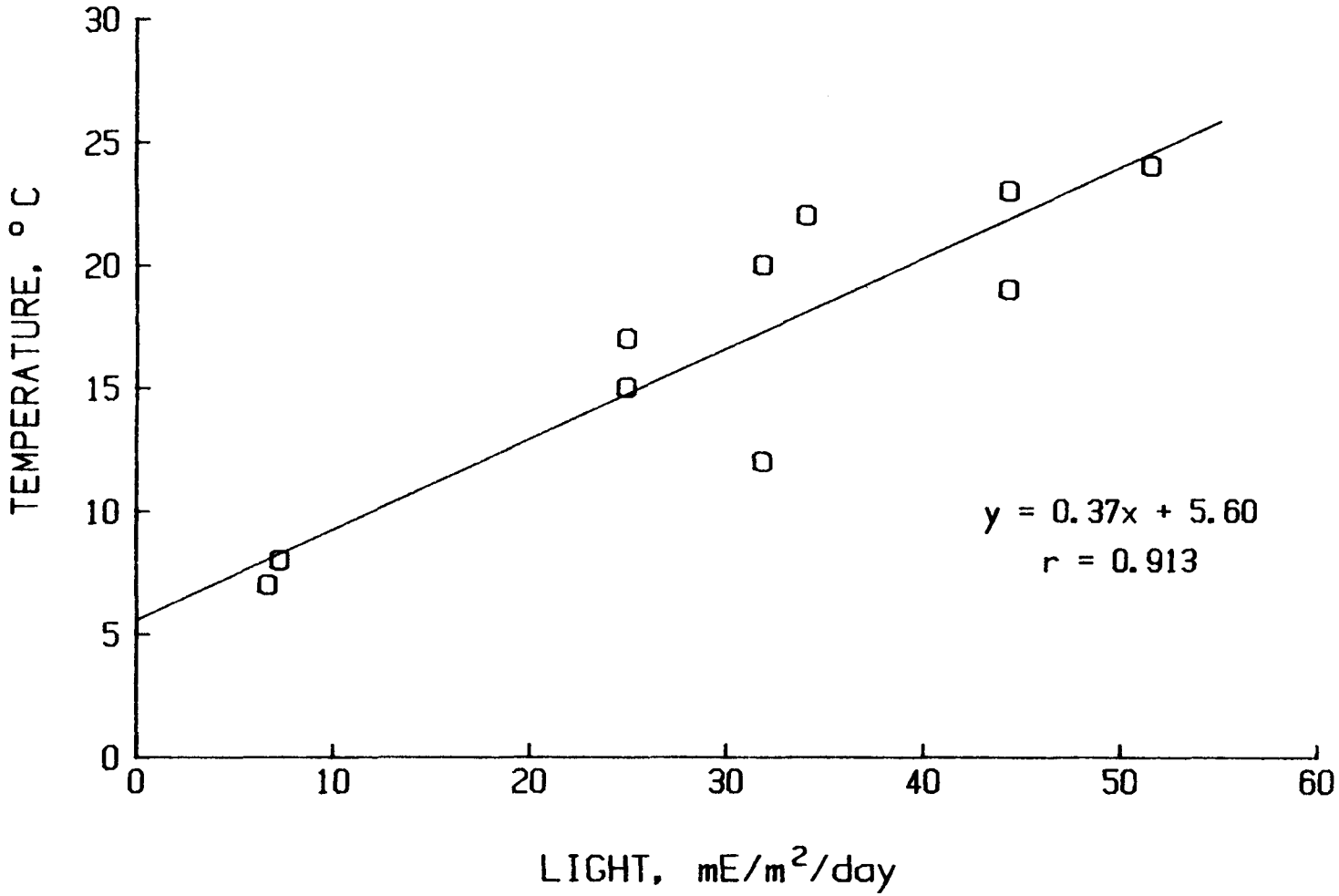

Fig. 8. Linear regression of maximum bottom-water temperatures on maximum incident light levels from the same time period, data were collected from 1981 to 1983.

exceeded 20°C, while in 1981 there were 8 days.

DISCUSSION

Results of this study (summarized in Table 20) confirmed distinct differences in plants previously observed in Izembek Lagoon (Dennison 1979, Iizumi et al. 1980, Short 1981). Plants in deep water (Station 8) had significantly larger biomass, LAI, leaf length, and significantly lower density than did plants in shallow water (Station 2). Mechanisms used by plants in response to clipping also differed between stations and between years of good and bad weather. All significant differences due to clipping appeared to be related to carbon allocation. There were some similarities in results of this study with those from naturally grazed seagrass beds, but changes observed in leaf growth rates, leaf biomass and shoot density were not typical of those reported for naturally grazed terrestrial plants.

Compensatory Growth

Grazing can stimulate growth in plants that have co-evolved with herbivores (McNaughton 1979, McNaughton et

Table 20. Summary of results of two-way ANOVA comparisons, significant differences (+), and non-significant differences (-) for main effects. Blank spaces indicate no comparison.

	Inter-annual		Seasonal			Clipping			Station	
Comparison	Clip	Control	Clip	Control	Clip v. Control	1981	1982	Pooled[1]	Clip	Control
Leaf biomass									+	+
Station 2	-	-	-	-				+		
Station 8	-	-	+	-				+		
Shoot density									+/+[2]	+/+
Station 2	-	-	-	-	+/-	+	-	-		
Station 8	+	+	-	-	-/-	-	-			
LAI									-/-	+
Station 2	+	-	-	-	-/-	+	-	+		
Station 8	-	-	-	-				+		
SLA									-	-/+
Station 2	-	+	+	-	+/-	-	+			
Station 8	-	-	-	-				-		
Longest leaf									+/-	+
Station 2	-	-	-	-				+		
Station 8	+	-	+	-	-/-	-	+	+		
Root-rhizome biomass									+/+	+
Station 2	+	-	-	-	+/+	+	-			
Station 8	+	-	-	-	+/-	-	-			
% C in leaves									+	+
Station 2							+			
Station 8							-			
% C in roots								+[3]	-	-
Station 2							-			
Station 8							-			
% N in leaves									-	-
Station 2							-			
Station 8							-			
% N in roots									-	-
Station 2							-			
Station 8							-			

[1] Data from 1981 and 1982 were pooled.
[2] +/- indicates two separate comparisons, 1981 and 1982.
[3] Data from both stations were pooled.

al. 1983). *Kyllinga nervosa*, a common terrestrial sedge in the relatively pristine Serengeti ecosystem, produces higher leaf biomass through rapid leaf elongation and increased tillering when grazed (McNaughton et al. 1983). Available nitrogen (often supplied by herbivores) commonly governs the ability of both *K. nervosa* and other grazed plants to regrow after repeated grazing (Risser and Parten 1982, Bryant et al. 1983, McNaughton et al. 1983).

Decreases in leaf growth rates after clipping occur only after severe defoliation in naturally grazed terrestrial plants; normally, high-nutrient reserves in storage organs of plants allow root growth to slow in favor of accelerated leaf growth (Youngner 1972). Plants which grow in low-nutrient environments cannot store high-nutrient reserves and must maintain root metabolism and uptake after clipping (Chapin and Slack 1979, Chapin 1980, Bryant et al. 1983), and compensatory regrowth can be reduced (Chapin and Slack 1979, McNaughton et al. 1983).

Leaf growth rates of the seagrass, *Thalassia testudinum*, decreased after plants were grazed by green turtles (*Chelonia mydas*; Zieman et al. 1984). The lack of an additional or allochthonous nitrogen supply could explain the inability of *T. testudinum* to increase growth

rates or sustain repeated grazing as compared with terrestrial plants. Because seagrasses inhabit an aquatic medium, nitrogen excreted by grazers does not remain in the grazed area; sediment nitrogen concentrations were significantly reduced in grazed plots of *T. testudinum* (Zieman et al. 1984).

The lack of either increased leaf growth rates or shoot densities in clipped plots in Izembek Lagoon could be due to nitrogen limitation. However, clipped plants did not have reduced nitrogen concentrations in either leaves or roots compared with control plants. Results of nitrogen uptake experiments, however, suggested that clipping could have created an increased nitrogen demand by leaves, especially at Station 2. If plants in Izembek Lagoon became nitrogen limited as a result of clipping, slow leaf growth rates could passively increase nitrogen content to levels typical of control plants. Increases in nitrogen content as a result of slow leaf growth rates have been reported in several species of marsh plants (Shaver and Mellilo 1984). Slow leaf growth rates could also aid in maintaining aerobic root metabolism if rates of photosynthesis did not decrease. Because seagrasses are rooted in anaerobic sediments, photosynthesis is required to supply oxygen to roots (Penhale and Wetzel 1983). The

amount of oxygen transported to roots has been positively correlated with shoot size in *Z. marina* (Smith et al. 1984), consequently, decreases in photosynthetic area as a result of clipping could decrease the total oxygen supply to the plant. In order to maintain an oxygenated root system, most oxygen would likely be allocated to roots for basic metabolism and nutrient uptake after clipping. Slow leaf growth rates could then be doubly beneficial to seagrasses after clipping by reducing both the oxygen and nutrient demand of the shoot.

Non-Structural Carbohydrate Reserves

While nutrient reserves govern the ability of terrestrial plants to regrow after grazing, non-structural carbohydrate (NSC) reserves determine how quickly growth will take place. New leaves generally import carbon from other parts of the plant (Watson and Casper 1984), therefore, plants with access to large quantities of NSC through adjacent organs or tillers, typically regrow more quickly after clipping than those which do not (Alberda 1966, Youngner 1972, Gifford and Marshall 1973). For many aquatic plants, NSC from rhizomes supply the initial carbohydrate requirements of spring growth (Good et al. 1982, Birch and Cooley 1983, Brock et al. 1983).

Experimental clipping of giant cutgrass, *Zizaniopses miliacea* and the seagrasses, *Posidonia oceanica* and *Thalassia testudinum*, indicate that ability to regrow was also determined by NSC in rhizomes (Birch and Cooley 1983, Wittmann and Ott 1982, Dawes and Lawrence 1979). In addition, NSC content of rhizomes has been positively correlated with root-rhizome biomass in *Typha spp.* and *Zizaniopsis miliacea* (Fiala 1978, Birch and Cooley 1983) suggesting that changes in root-rhizome biomass are indicative of changes in rhizome reserves. *Zostera marina* rhizomes are known to contain substantial amounts of sucrose alone (25-30 % of dry wt [Drew 1979]) which could be allocated to other parts of the plant after clipping.

In Izembek Lagoon, decreases in root-rhizome biomass in control plots in early summer (1982) were accompanied by increases in carbon concentration in leaves. The opposite pattern was observed in late-summer, suggesting that carbon was allocated to and from rhizomes (Fig. 9). Mobilization of stored NSC reserves from rhizomes was probably most important early in summer because leaf growth rates in *Z. marina* were highest during this time. As leaf growth rates slowed in mid-summer, carbon concentrations in leaves and roots rose. Increases in carbon content could be due to high rates of

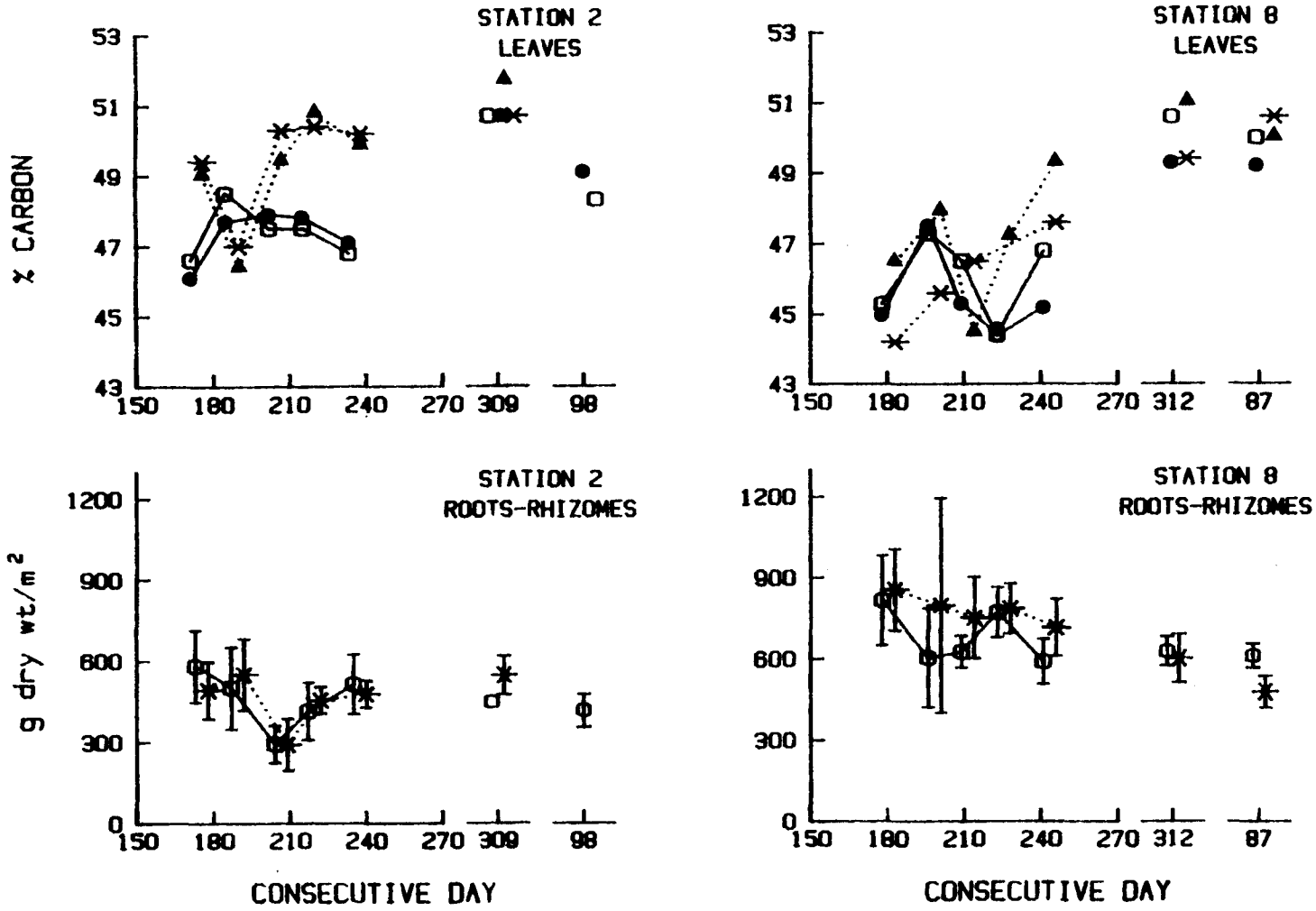

Fig. 9. Comparison of carbon content of leaves with root-rhizome biomass from Stations 2 and 8 for 1982-1983. Data presented as in Figs. 5 and 6.

photosynthesis which typically peak in mid-summer (McRoy 1974). High rates of photosynthesis are probably related to increases in water temperatures which also reach a maximum in mid-summer; at temperatures above 20°C and saturation light intensities, rates of photosynthesis rise considerably without a corresponding rapid increase in respiration (Biebl and McRoy 1971, McRoy 1974, Drew 1979). The resulting net increase in fixed carbon during warm, bright weather could permit plants to accumulate NSC in rhizomes.

Carbon Allocation: 1982

By mid-summer, carbon concentrations of leaves in the clipped plot at Station 2 were significantly higher than those of control plants. Very high carbon content in leaves of clipped plants when average temperatures were highest, probably resulted from a combination of high rates of net photosynthesis and slow leaf growth. Carbon is also required for new shoot production, therefore increases or decreases in the rates of shoot initiation could affect the carbon content of leaves. Shoot density data indicated that densities did not differ in clipped and control plots, suggesting that in both plots shoot initiation equally balanced shoot death. There was no

indication of whether shoots were longer- or shorter-lived as a result of clipping.

Root-rhizome biomass in clipped and control plots at Station 2 were very similar in 1982, suggesting that reserves in rhizomes were not used by plants in 1982 in response to clipping. In years for which physical conditions (e.g., light and temperature) are comparatively good, the potential for allocation of reserves to rhizomes could be greater. For example, in the saltmarsh plant, *Spartina sp.*, belowground biomass peaks earlier in late summer in plants from low latitudes, where conditions for growth are more favorable and rhizome reserves are less crucial, compared with *Spartina sp.* from higher latitudes (Good, et al. 1982). If shoots begin to grow earlier or net photosynthetic rates are high, allocation to rhizomes could begin earlier. Comparing late summer root-rhizome biomass data from Station 2 during 1981 and 1982 suggested earlier allocation to rhizomes in 1982. Comparisons of light and temperature data also indicated that environmental conditions were more favorable in 1982 than in 1981. Finally, there was a significant increase in root-rhizome biomass of clipped plants from 1981 to 1982, as well as an increase (not significant) in control plants, suggesting that more carbon was available for

allocation to rhizomes in 1982. Weather conditions, that apparently led to high rates of net photosynthesis, could have allowed plants at Station 2 to rely primarily on photosynthesis and not rhizome reserves as a source of carbon for regrowth after clipping.

Both carbon concentrations and root-rhizome biomass were more variable within the year at Station 8 than at Station 2. Comparisons between stations showed that carbon contents of leaves from both clipped and control plants were significantly lower at Station 8. Large, deep-water *Z. marina* have lower rates of photosynthesis than small, shallow-water plants at the same temperature (Dennison and Alberte 1982), therefore, lower rates of photosynthesis at Station 8 could result in significantly lower carbon concentrations in leaves compared with Station 2. However, the relationship between seasonal changes in carbon content in leaves and root-rhizome biomass observed at Station 2 was also apparent at Station 8.

Clipped plants at Station 8 had a lower percentage of control leaf biomass after ten days regrowth than did plants at Station 2. As a result, reduction in photosynthetic area was relatively more severe at Station 8. Despite large losses of leaf biomass, plants at Station 8 showed little change in carbon content of leaves after

clipping, with the exception of a change in pattern in new leaves compared with plants from control plots. There was also no decrease in shoot density as a result of clipping, indicating that shoot initiation did not slow with respect to shoot mortality.

Root-rhizome biomass in clipped plots decreased steadily throughout the summer, but not in a pattern similar to plants in control plots. Seasonal effects were statistically significant for root-rhizome biomass in all study plots, except for the comparison of clipped and control plots at Station 8 in 1982 (Table 20). Significant seasonal effects were produced by consistent patterns of high biomass in spring and late summer and low biomass in mid-summer. The slow, consistent decline in biomass in the clipped plot caused the absense of a significant seasonal effect in 1982 at Station 8. Decreasing root-rhizome biomass in the clipped plot corresponded well with increasing carbon content of new leaves. Plants at Station 8 could have responded to clipping as do seagrasses that are naturally grazed (Dawes and Lawrence 1979, Zieman et al. 1984) by slowing leaf growth rates and drawing steadily upon storage reserves.

Carbon Allocation: 1981

There are no data for carbon content in 1981, but comparisons of root-rhizome biomass between years suggested a different response to clipping in the first year of the study compared with the second. At Station 2, there was a significant decrease in root-rhizome biomass in the clipped compared with the control plot, indicating that rhizome reserves were important as a response to clipping. As mentioned above, rhizome biomass in general did not increase until quite late in summer in 1981, and several other differences, including changes in weather conditions between years were noted as well. Longest leaves and LAI were smaller in the clipped plots in 1981 compared with 1982, and while these differences may reflect differences in clipping technique, they could also indicate that clipped leaves did not grow as quickly in 1981. Shoot densities in 1981 were consistently (but not significantly) lower in clipped compared with control plots. These data suggested that shoot initiation rates could have been lower in clipped plots. Combined, these features suggested that clipped plants were relatively carbon limited in 1981 compared with 1982, and this limitation led to significant decreases in rhizome reserves.

At Station 8, none of the differences observed at Station 2 in 1981 between clipped and control plots were evident. There was no decrease in root-rhizome biomass as a result of clipping, and no evident change in response in the leaf canopy between years. Unlike those at Station 2, plants from the clipped plot at Station 8 did not appear to be more carbon limited than control plants in 1981.

Inter-Annual Variation, 1963-1982

Inter-annual variation was significant in Izembek Lagoon as it is in most natural communities and ecosystems (Sutherland 1981, Sousa 1984b). Consequently, the effects of disturbance (clipping) should be evaluated within the context of natural oscillations (Likens 1985). The *Z. marina* beds surrounding Station 8 have been studied periodically from 1963-1982. Biomass data from this area offer some indication of the pattern of annual variation and eelgrass bed development over a 20-year period (Figs. 10 and 11).

Root-rhizome biomass fluctuated considerably over 20 years (e.g., see mid-August data, Fig. 10). The low mean root-rhizome biomass recorded in 1964 (McRoy 1966) was also highly variable within the sampling site, suggesting that plant density was patchy. Nine years later,

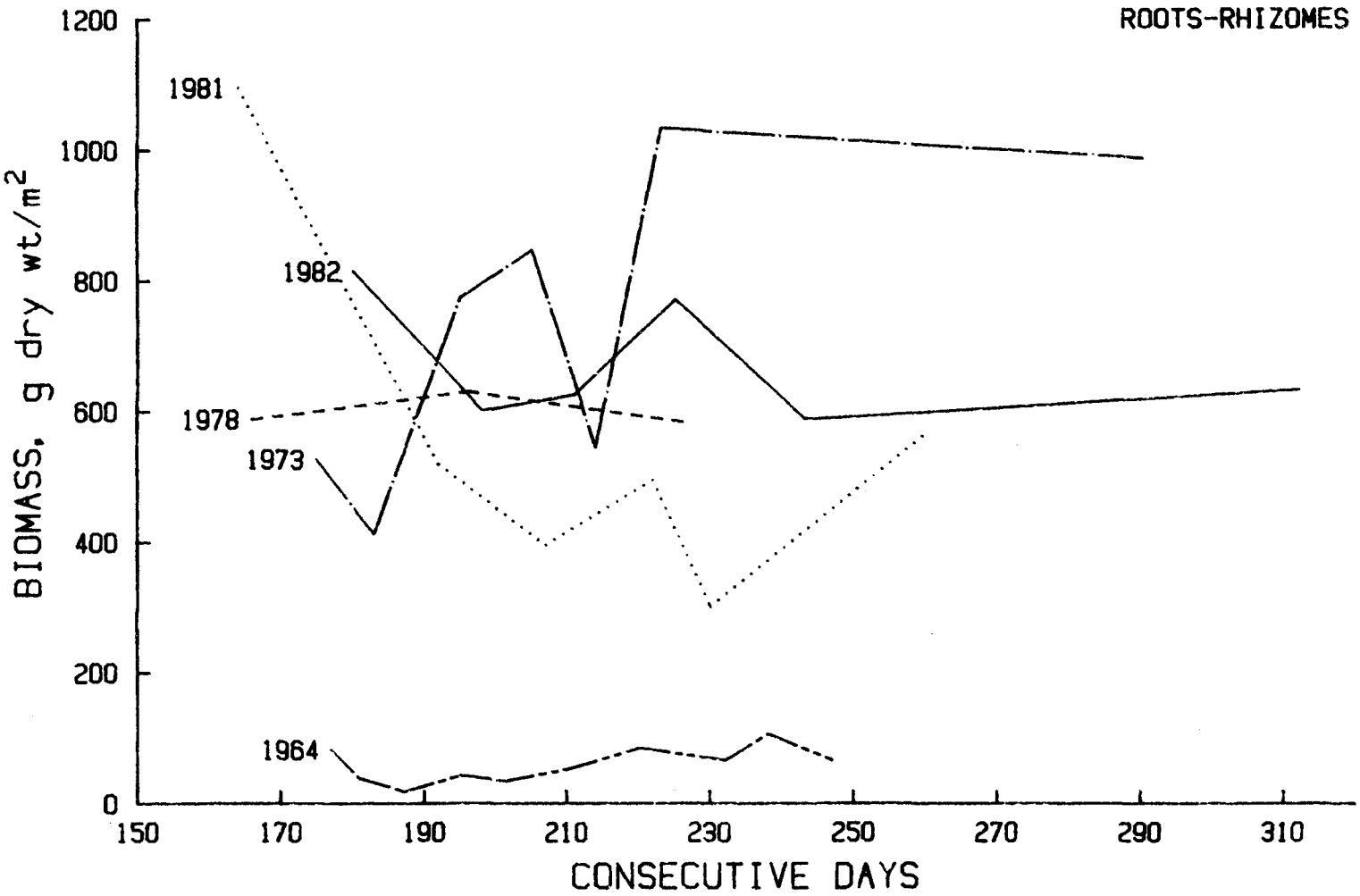

Fig. 10. Seasonal trends in mean root-rhizome biomass (g dry wt·m^{-2}) collected in the vicinity of Station 8. Data are from the following sources: 1964 (McRoy 1966); 1973 (McRoy *unpublished*); 1978 (Dennison 1979); 1981 and 1982, from control plots, this study. Day 152 is June 1.

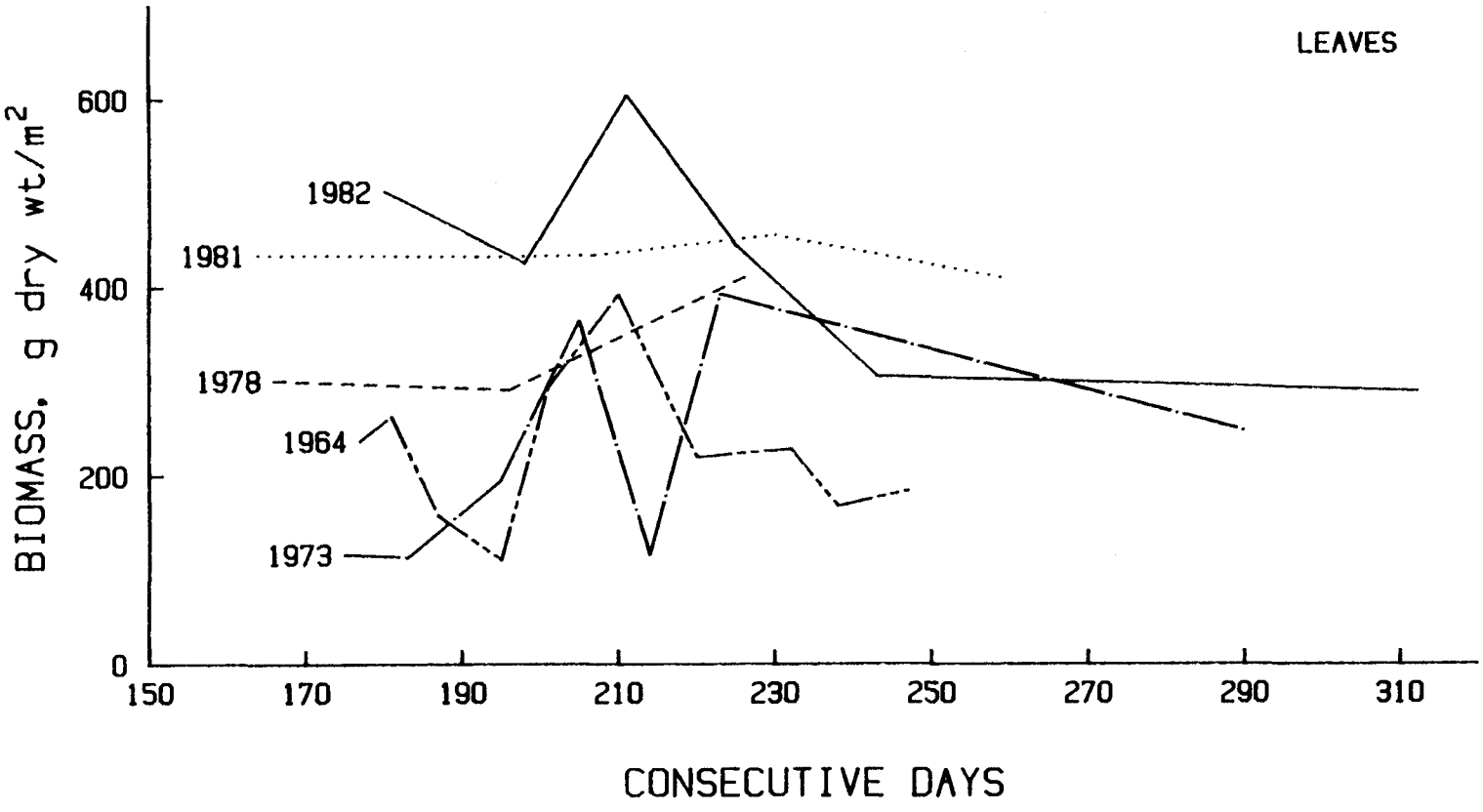

Fig. 11 Seasonal trends in mean leaf biomass (g dry wt·m^{-2}) collected in the vicinity of Station 8. Data are from the following sources: 1964 (McRoy 1966); 1973 (McRoy *unpublished*); 1978 (Dennison 1979); 1981 and 1982, from control plots, this study. Day 152 is June 1.

root-rhizome biomass was much greater and within site variability had decreased, indicating that plant cover was more uniform. Since 1973, root-rhizome biomass has decreased and become less variable between succesive years. A seasonal biomass pattern has emerged, suggesting that an equilibrium has developed between carbohydrate reserves (root-rhizome biomass) and leaf growth requirements.

Conversely, leaf biomass increased slowly and steadily over the 20-year period (Fig. 11). Seasonal fluctuations moderated as biomass increased. Biomass data collected during this study were the highest recorded for this station, suggesting that leaf biomass may continue to increase and possibly "overshoot" equilibrium levels (Horn 1974).

The ratio of below- to above-ground biomass (root-rhizome to leaf ratio) is often used as an indicator of nutrient-limited (high root-rhizome to leaf ratio) or light-limited (low root-rhizome to leaf ratio) growth in terrestrial ecosystems (Mooney 1972, Harper 1977, Grime 1979). The highest root-rhizome to leaf ratio at Station 8, 3.19, occurred in 1973 (Table 21).

Seagrasses can be nutrient limited. Applications of fertilizer increased biomass of *Z. marina* in Chesapeake

Table 21. Leaf biomass, root-rhizome biomass, and root-rhizome to leaf ratios (g dry wt·m^{-2}) from plants sampled during the growing season in the vicinity of Station 8 in Izembek Lagoon. Data are means and standard deviations from the following sources: 1964, n=10, McRoy 1966; 1973, n=6, McRoy *unpublished*; 1978, n=3, Dennison 1979; 1981, n=5 and 1982, n=5, from this study.

Year	Leaves	Roots-rhizomes	R-R/L
1964	225	59	0.26
s.d.	80	27	
1973	216	690	3.19
s.d.	130	234	
1978	335	600	1.79
s.d.	68	27	
1981	433	562	1.30
s.d.	17	278	
1982	456	672	1.49
s.d.	110	96	

Bay, USA (Orth 1977), and increased growth rates of leaves of *Heterozostera tasmanica* in Australia (Bulthius and Woelkerling 1981). It has been suggested that growth of *Z. marina* at Station 2 is nitrogen limited (Short 1981); the mean root-rhizome to leaf ratio, 3.3, at Station 2 was similar to that documented at Station 8 in 1973.

Data from 1982 indicated a low root-rhizome to leaf ratio and, therefore, light-limited growth at Station 8. Other work done at this station also suggests that plants at Station 8 are light limited (Dennison 1979). Theoretically, light-limited growth as a result of self-shading, is typical of well developed seagrass beds (McRoy and McMillan 1977).

Data from 1963-1982 suggest that the *Z. marina* bed at Station 8 developed from a sparsely populated area, through a nutrient limited stage closely resembling the 1981-1982 study site at Station 2. With continued accumulation of organic sediments and plant growth, the site gradually developed to the point at which plant growth was limited by self-shading (Dennison 1979). This scenario suggests that inter-annual differences can include different growth and allocation strategies at the same study site as well as between sites. These changing strategies could represent a successional sequence that

results from ecosystem development.

Seasonal biomass data from Station 2 are available only from 1978 (Dennison 1979) and this study. In general, however, shallow-water or near-shore plant stands are characterized by short plants, a feature that is apparently independent of the age of the bed (Keller and Harris 1966, Harrison and Mann 1975, Jacobs 1979, Dennison and Alberte 1982). These data, coupled with the great similarity in biomass of plants from control plots from 1981 to 1982 in this study, suggested that the *Z. marina* bed at Station 2 is not undergoing the same developmental changes postulated for Station 8.

Disturbance

Successional processes seldom proceed uninterrupted to climax communities (Sutherland 1981, Sousa 1984b, Likens 1985). Disturbances of various proportions either check succession completely or maintain mosaics of successional diversity. The importance of disturbance has been reported for both marine (Dethier 1984, Paine 1984, Sousa 1984a, Kirkman 1985, Turner 1985) and terrestrial (Bormann and Likens 1979, Sprugel and Bormann 1981, Romme 1982, Likens 1985) systems. If plants at Station 2 are held at an "earlier" successional state compared with

plants at Station 8, there should be some intrinsic difference in type or rate of disturbance between the two stations.

Seagrasses typically populate sheltered embayments. Despite this environment, physical disturbances, particularly wave action during seasonal storm periods (Kirkman 1985) and ice scouring (Short 1983a), can be important in determining how rapidly a seagrass bed will reach typical climax composition, if at all. There are distinct differences in *Zostera marina* growing in areas of relatively high versus low wave disturbance (Harrison and Mann 1975). Particularly obvious was the presence of "tall plants at all depths up to the low tide mark" at the calmer site (Harrison and Mann 1975).

Marine plants and animals that inhabit the shallow subtidal or intertidal have characteristic features that enable them to persist in areas of high wave impact (Santelices et al. 1980, Koehl 1982). For plants with frond-like growth forms, the effect of depth is particularly important, because increasing depth decreases the impact of flow. Since a small increase in leaf length creates a relatively large increase in form drag (Koehl 1982) shallow-water plants are more likely to be small and have multiple stipes (Santelices et al. 1980). Plants can

also ameliorate drag by flexibility, since flow is slower near the bottom (Koehl 1982).

For *Z. marina* in Izembek Lagoon, wave action is potentially more severe for plants in shallower water (Station 2) than it is for those in deeper water (Station 8). Gas-filled leaf lacunae tend to make plants float to the surface where leaves are more subject to wave damage. Deep-water plants spend relatively little time in water depths less than leaf length, while shallow-water plants are generally in depths of less than 50 cm. These differences in water depth were particularly noticeable in November when weather conditions were stormy and lower low tides were high compared with summer tides. Higher low tides buffered wave impact at Station 8 but not at Station 2.

In addition to wave disturbance, plants in shallow water tide pools are also affected by accumulating grass wrack. Large mats of floating wrack can become entangled with live plants at low tide, uprooting them or blocking out light.

Because of the importance of long-term information in assigning a successional state to a given area, it was impossible to determine whether short plants with relatively high root-rhizome to leaf ratios at Station 2

represented a *Z. marina* bed adapted to wave disturbance, held indefinitely at an intermediate successional state, or a *Z. marina* bed moving through nutrient limited conditions toward an equilibrium point resembling that at Station 8.

CONCLUSIONS

Plants at both deep- and shallow-water stations in Izembek Lagoon were quite stable with respect to disturbance from clipping. There was no indication that clipping led or was leading to a change in successional state at either station. Because no change in successional state was observed, resilience could not be evaluated. Both plant stands appeared to require substantial disturbance, probably including disruption of entire plants and sediment, before successional state is altered.

Z. marina beds at Stations 2 and 8 can be easily distinguished by significant differences in total biomass, leaf canopy and carbon concentration. Plants at the two stations are also rooted in sediments of different organic and nutrient content (Iizumi et al. 1980, Short 1983b), but despite these clear distinctions, clipping experiments

indicated that plants at Stations 2 and 8 did not fall into the separate categories used to describe strategies of growth in functionally different terrestrial plants (e.g., r and K reproductive strategies [MacArthur and Wilson 1967] or ruderal, stress tolerant, and competitor growth strategies [Grime 1979]). Life in the marine environment has placed constraints on seagrasses (den Hartog 1977) that apparently are not comparable to those of terrestrial systems.

The most important of these constraints could be that photosynthesis supplies the total oxygen requirement of all belowground plant biomass. Because oxygen demand and photosynthesis are linked, overall plant growth can be affected by the potential for anaerobic metabolism in roots. In Izembek Lagoon, strong seasonal signals and inter-annual variation in the physical environment also affect photosynthetic rates, growth, and carbon allocation, and as a result, plants must be adapted to conditions that encompass a wide range of possibilities. The rigors of a strongly seasonal and variable marine environment could limit the options available for plant growth strategies.

It seems clear that the *Z. marina* stand at Station 8 has progressed through several stages that resemble those

of terrestrial ecosystem development. However, comparisons of Stations 2 and 8 did not suggest different growth strategies as would be expected from plants in different stages of succession in a terrestrial ecosystem (Grime 1979). Plants from control plots at both stations had similar seasonal patterns of change in biomass, leaf growth rates, and carbon and nitrogen content. Differences were likely to be seen in terms of relative magnitude but not in the direction of change. Because the marine environment requires specific adaptations, and plant succession in the *Z. marina* ecosystem appears to occur through changes in root-rhizome to leaf ratio in a single species (Table 21), plants in well developed stands could retain many characteristics of plants in earlier successional stages.

Of the differences observed in this study, alterations in growth rate and carbon allocation (suggested by changes in biomass and carbon content) were the most prominent means by which plants adjusted to the loss of photosynthetic area through clipping. However, physical and biological factors which could alter the plants' abililty to photosynthesize or translocate carbon, could also affect the response to clipping. In addition to slow leaf growth rates, there were two mechanisms through

which clipped plants could have maintained sufficient carbon concentrations: 1) utilization of carbohydrates recently produced in leaves (when rates of photosynthesis were high) and 2) mobilization of carbohydrate reserves stored in rhizomes.

These suggested mechanisms appeared to be adopted differently by plants at Stations 2 and 8 due to differences in root-rhizome to leaf ratios and weather conditions. While plants in both clipped plots slowed leaf growth rates, clipped plants at Station 2 appeared to draw mainly upon root-rhizome biomass in 1981, and photosynthesis in 1982, as sources of energy for regrowth and maintenance. In 1982, clipped plants at Station 8 seemed to rely upon root-rhizome biomass; the response to clipping in 1981 was not clear.

The ability of plants at either station to accumulate root-rhizome biomass (and probably carbohydrate reserves) appeared to be related to the proportion of photosynthetic area to belowground biomass. The longer-leaved plants in the control plots at Station 8 showed considerable variability in root-rhizome biomass while plants at Station 2 were more consistent between years. Since the ability of leaves to grow long is important to decreasing the root-rhizome to leaf ratio, wave disturbance in

shallow water could indirectly dictate root-rhizome to leaf ratios by keeping leaves short. This suggests that the *Z. marina* bed at Station 2 could be maintained at approximately the same root-rhizome to leaf ratio through an equilibrium with the physical environment. The similarities in root-rhizome to leaf ratios between plant stands at Station 2 during this study and those at Station 8 in 1973 suggested that a short, dense leaf canopy could be a phase of ecosystem succession. However, the influence of wave action at Station 2 also suggests that the same root-rhizome to leaf ratios could be produced by physical features of the environment.

Although clipping at Stations 2 and 8 produced different changes in root-rhizome biomass and carbon concentration, the results of this study did not indicate that shallow-water plants in Izembek Lagoon were necessarily in an earlier successional state as compared with those in deeper water. Disturbance from wave action could maintain a high root-rhizome to leaf ratio in shallow-water plant stands despite sediment development. Data collected through 18 years from plants in deeper water suggested that a temporal sequence of changes in root-rhizome to leaf ratios, typical of terrestrial ecosystem succession, can occur in deeper water.

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APPENDIX 1.

Data from Station 2, 1981-1983: leaf biomass (g dry wt $\cdot m^{-2}$), n=5; SLA ($cm^2 \cdot g^{-1}$ dry wt leaf); root-rhizome biomass (g dry wt $\cdot m^{-2}$), n=5; carbon content (% of ash free dry wt); nitrogen content (% of ash free dry wt). Dates are 1981/1982; April data are from 1983.

	Date							
	13/22 June	12/6 July	23/23 July	12/5 August	19/23 August	21 September	5 November	8 April
Leaf biomass (mean +/- s.d.)								
1981								
Control	86	140	128	145	143	100	-	-
s.d.	16	56	32	20	40	27	-	-
Clipped	-	62	59	99	69	57	-	-
s.d.	-	25	6	25	28	18	-	-
1982-1983								
Control	198	205	100	170	160	-	146	50
s.d.	32	38	20	32	26	-	26	10
Clipped	143	134	62	95	128	-	93	-
s.d.	22	9	10	13	18	-	16	-
SLA (replicates)								
1981								
Control	204	190	190	158	197	-	-	-
	210	203	180	143	-	-	-	-
Clipped	-	201	177	151	179	-	-	-
	-	187	183	-	-	-	-	-
1982								
Control	258	249	243	235	239	-	132	-
	225	254	253	232	241	-	148	-
Clipped	-	239	219	219	224	-	110	-
	-	205	224	216	204	-	110	-
Root-rhizome biomass (mean +/- s.d.)								
1981								
Control	645	401	310	343	275	495	-	-
s.d.	170	61	28	66	19	177	-	-
Clipped	-	306	234	267	249	461	-	-
s.d.	-	61	46	12	57	167	-	-
1982-1983								
Control	581	500	293	414	513	-	448	417
s.d.	133	152	68	105	110	-	31	61
Clipped	492	550	291	454	477	-	549	-
s.d.	105	132	95	49	50	-	74	-

APPENDIX 1. Cont.

	Date							
	13/22 June	12/6 July	23/23 July	12/5 August	19/23 August	21 September	5 November	8 April
Carbon content: 1982-1983 (replicates)								
New leaves								
Control	46.6	47.5	47.5	46.2	46.7	-	50.9	48.1
	46.5	49.6	47.4	48.7	46.9	-	50.6	48.4
Clipped	49.5	46.8	50.4	50.4	49.9	-	51.0	-
	49.4	47.1	50.1	50.3	50.5	-	50.4	-
Old leaves								
Control	46.1	47.7	47.9	48.4	47.0	-	50.9	49.4
	46.1	47.8	48.0	47.2	47.2	-	50.6	48.8
Clipped	48.6	46.2	49.5	50.9	50.6	-	50.5	-
	49.4	46.5	49.3	50.7	50.2	-	51.9	-
Roots								
Control	44.6	45.7	45.9	46.5	45.2	-	39.1	44.8
	44.8	44.2	46.2	45.1	45.4	-	39.4	41.8
Clipped	40.8	43.8	44.9	45.8	42.4	-	45.2	-
	41.3	44.0	44.7	46.2	42.1	-	43.7	-
Nitrogen content: 1982-1983 (replicates)								
New leaves								
Control	2.65	2.84	2.11	2.57	2.49	-	2.90	5.26
	2.17	2.80	2.05	2.57	2.28	-	2.87	5.19
Clipped	2.73	2.35	2.19	2.00	2.30	-	2.33	-
	2.75	2.16	2.23	1.97	2.31	-	2.28	-
Old leaves								
Control	1.82	2.23	1.46	1.75	1.53	-	2.19	3.79
	1.94	2.21	1.43	1.63	1.53	-	2.07	3.66
Clipped	1.76	1.61	1.54	1.29	1.48	-	1.43	-
	1.51	1.66	1.50	1.42	1.61	-	1.75	-
Roots								
Control	1.31	1.61	1.38	1.02	1.24	-	1.37	1.64
	1.27	1.43	1.59	1.01	1.22	-	1.36	1.45
Clipped	1.14	1.30	1.21	1.52	1.38	-	1.46	-
	1.22	1.28	1.14	1.51	1.35	-	1.21	-

APPENDIX 2.

Data from Station 8, 1981-1983: leaf biomass (g dry wt $\cdot m^{-2}$), n=5; SLA ($cm^2 \cdot g^{-1}$ dry wt leaf); root-rhizome biomass (g dry wt $\cdot m^{-2}$), n=5; carbon content (% of ash free dry wt); nitrogen content (% of ash free dry wt). Dates are 1981/1982; March data are from 1983.

	Date							
	13/29 June	11/17 July	26/30 July	10/13 August	18/31 August	20 September	8 November	28 March
Leaf biomass (mean +/- s.d.)								
1981								
Control	434	433	434	-	455	408	-	-
s.d.	130	178	211	-	121	60	-	-
Clipped	-	158	114	101	93	70	-	-
s.d.	-	46	15	27	20	23	-	-
1982-1983								
Control	502	425	604	444	305	-	288	125
s.d.	194	90	175	59	57	-	34	41
Clipped	247	220	234	120	103	-	78	62
s.d.	99	30	31	30	24	-	23	18
SLA (replicates)								
1981								
Control	174	181	202	171	203	-	-	-
	189	182	205	171	182	-	-	-
Clipped	-	189	172	175	187	-	-	-
	-	169	181	173	-	-	-	-
1982								
Control	202	234	220	151	208	-	115	-
	213	233	205	174	190	-	117	-
Clipped	191	224	177	171	169	-	122	-
	190	216	167	173	157	-	112	-
Root-rhizome biomass (mean +/- s.d.)								
1981								
Control	1096	519	395	494	301	565	-	-
s.d.	166	129	92	57	15	79	-	-
Clipped	-	507	315	494	389	604	-	-
s.d.	-	154	83	55	46	205	-	-
1982-1983								
Control	815	602	625	770	588	-	632	612
s.d.	165	182	59	92	83	-	54	45
Clipped	854	795	750	784	714	-	602	476
s.d.	150	396	150	91	105	-	89	59

APPENDIX 2. Cont.

	Date							
	13/29 June	11/17 July	26/30 July	10/13 August	18/31 August	20 September	8 November	28 March
Carbon content: 1982-1983 (replicates)								
New leaves								
Control	42.4	46.5	47.2	44.7	46.7	-	50.8	50.2
	48.1	48.0	45.9	44.2	46.9	-	50.5	49.8
Clipped	44.2	45.5	46.2	-	47.7	-	49.9	50.8
	44.2	45.7	46.7	-	47.5	-	48.8	50.3
Old leaves								
Control	46.1	48.5	45.2	44.8	45.5	-	49.9	49.6
	44.0	46.5	45.4	44.0	44.9	-	48.8	48.5
Clipped	46.6	47.2	43.5	48.2	49.5	-	51.5	49.9
	46.3	48.5	45.4	46.3	49.0	-	50.5	50.2
Roots								
Control	40.7	46.6	44.8	43.7	44.5	-	43.1	43.6
	39.5	46.6	45.1	44.1	45.0	-	41.8	42.2
Clipped	42.7	43.7	42.3	41.7	45.6	-	45.3	43.5
	41.1	42.2	42.8	42.4	45.2	-	45.2	42.5
Nitrogen content: 1982-1983 (replicates)								
New leaves								
Control	2.15	2.16	2.27	2.46	2.46	-	3.03	4.84
	2.71	2.21	2.30	2.43	2.65	-	3.04	4.96
Clipped	2.05	2.65	2.34	-	2.01	-	2.72	5.37
	2.02	2.65	2.39	-	2.01	-	2.54	5.94
Old leaves								
Control	2.01	1.65	1.79	1.62	1.71	-	2.60	3.72
	1.78	1.61	1.64	1.70	1.71	-	2.44	3.64
Clipped	1.74	1.97	1.52	1.89	1.42	-	2.16	4.64
	1.65	2.05	1.59	1.59	1.40	-	2.04	4.96
Roots								
Control	1.14	1.37	1.16	1.24	1.14	-	1.18	1.34
	1.17	1.25	1.17	1.45	1.07	-	1.19	1.32
Clipped	1.44	1.30	1.34	1.28	1.06	-	1.23	1.36
	1.48	1.23	1.38	1.41	1.11	-	1.23	1.40

APPENDIX 3.

Daily totals of incident light ($mEin \cdot m^{-2} \cdot day^{-1}$) at Izembek Lagoon, 1981-1983.

Date	Year		
	1981	1982	1983
26 March	-	-	15.1
27 March	-	-	15.1
28 March	-	-	15.4
29 March	-	-	10.8
30 March	-	-	13.9
31 March	-	-	20.5
1 April	-	-	31.8
2 April	-	-	27.0
3 April	-	-	11.3
4 April	-	-	16.5
5 April	-	-	11.8
6 April	-	-	22.9
7 April	-	-	22.9
8 April	-	-	10.5
9 April	-	-	5.5
10 April	-	-	11.1
11 April	-	-	34.0
12 April	-	-	30.7
13 April	-	-	30.7
14 April	-	-	17.5
15 April	-	-	24.1
16 April	-	-	22.6
17 April	-	-	41.6
14 June	35.5	-	-
15 June	14.8	-	-
16 June	28.9	-	-
17 June	26.8	-	-
18 June	59.1	-	-
19 June	16.8	47.6	-
20 June	13.8	11.0	-
21 June	16.8	37.5	-
22 June	30.9	19.2	-

APPENDIX 3. Cont.

Date	1981	1982	1983
23 June	24.8	22.4	-
24 June	-	38.5	-
25 June	16.7	12.2	-
26 June	46.2	21.4	-
27 June	46.2	21.4	-
28 June	-	32.1	-
29 June	-	32.1	-
30 June	-	41.6	-
1 July	-	18.9	-
2 July	-	9.9	-
3 July	-	34.6	-
4 July	-	34.0	-
5 July	-	16.2	-
6 July	-	11.6	-
7 July	-	33.5	-
8 July	-	55.6	-
9 July	27.1	21.9	-
10 July	33.4	61.2	-
11 July	23.8	56.1	-
12 July	25.4	13.8	-
13 July	29.8	19.7	-
14 July	20.6	25.1	-
15 July	20.6	23.2	-
16 July	26.9	15.5	-
17 July	13.0	17.1	-
18 July	19.8	17.5	-
19 July	51.5	44.0	-
20 July	49.0	54.7	-
21 July	50.5	22.6	-
22 July	39.0	12.4	-
23 July	19.6	28.7	-
24 July	35.5	27.4	-
25 July	36.0	29.0	-
26 July	43.1	12.7	-
27 July	24.5	17.2	-
28 July	42.8	14.1	-
29 July	34.0	20.7	-
30 July	27.1	42.9	-
31 July	18.4	42.7	-
1 August	24.9	31.8	-
2 August	24.9	31.4	-

APPENDIX 3. Cont.

Date	1981	1982	1983
3 August	24.9	17.6	-
4 August	31.5	16.5	-
5 August	13.4	50.7	-
6 August	38.4	44.1	-
7 August	35.6	10.9	-
8 August	17.4	23.2	-
9 August	33.7	20.3	-
10 August	19.7	31.4	-
11 August	19.7	24.5	-
12 August	37.3	24.5	-
13 August	14.3	35.9	-
14 August	24.7	36.7	-
15 August	54.4	20.2	-
16 August	13.0	29.0	-
17 August	16.3	29.0	-
18 August	36.0	18.7	-
19 August	25.5	41.7	-
20 August	26.6	44.3	-
21 August	34.4	17.8	-
22 August	34.4	12.4	-
23 August	-	14.1	-
24 August	-	14.9	-
25 August	-	14.9	-
26 August	-	15.0	-
27 August	-	10.1	-
28 August	-	10.1	-
29 August	-	23.8	-
30 August	-	11.5	-
31 August	-	20.7	-
1 September	-	24.9	-
2 September	-	24.9	-
3 September	-	24.9	-
4 September	-	9.4	-
5 September	-	8.5	-
6 September	-	7.1	-
7 September	-	16.2	-
3 November	-	4.1	-
4 November	-	7.6	-
5 November	-	6.7	-

APPENDIX 3. Cont.

Date	1981	1982	1983
6 November	-	4.9	-
7 November	-	1.6	-
8 November	-	5.9	-
9 November	-	3.4	-
10 November	-	6.4	-
11 November	-	1.4	-
12 November	-	5.3	-
13 November	-	6.5	-
14 November	-	6.5	-
15 November	-	2.8	-
16 November	-	3.5	-
17 November	-	7.3	-
18 November	-	6.2	-
19 November	-	5.6	-